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STUDIES ON *TRICULA APERTA* AND RELATED TAXA, THE SNAIL INTERMEDIATE HOSTS OF *SCHISTOSOMA MEKONGI*. I. GEOGRAPHICAL DISTRIBUTION AND HABITATS

Viroj Kitikoon, Santasiri Sornmani and Curt R. Schneider

ABSTRACT

The geographical distribution and habitats were determined for the so-called alpha, beta and gamma races of *Tricula aperta*, two other unnamed phenotypic taxa (pigmented and non-pigmented) of *T. aperta*, and *Manningiella* (? = *Tricula*) *conica*. The alpha and gamma races were found in the Mekong River, ranging from Ban Sabouxai, Savannakhet Province, Laos, to Ban Dan, Ubon Province, Thailand; the gamma race extended to Sompamit Falls in southern Laos as well, and possibly to Kratié in Cambodia; the beta race of *T. aperta* occurred exclusively in the Mune River (a tributary of the Mekong) at Phibun, Thailand. The two unnamed phenotypes of *T. aperta* were found only in the Mekong River above Sompamit Falls near the Laos-Cambodia border. *M. conica* was found in the Mekong River, mainly in front of Moung Khong Hospital, Khong Island, Laos. All of these snails preferred to live only on solid substrates. They may live at various depths and occur in either quiet or swiftly flowing water.

INTRODUCTION

Human schistosomiasis was first reported on the Southeast Asian mainland by Vic-Dupont (1957). Previously, this area was believed to be free from this serious human snail-transmitted parasitic disease. It was assumed that the parasite was *Schistosoma japonicum* Katsurada (Barbier, 1966; Audebaud et al., 1968; Pathammavong, 1969; Kitikoon, 1970; Iijima et al., 1971; Sornmani et al., 1971), the causative agent of schistosomiasis on the China mainland and in Japan, the Philippines and Celebes. However, the snail intermediate hosts, any subspecies of *Oncomelania hupensis* Gredler, were not known to occur in the Cambodia-Laos-Thailand region.

Because of this newly discovered health problem in Southeast Asia, various efforts in Thailand were directed toward the study of the parasite and its host, including a general malacological survey and search for the intermediate snail hosts. After various attempts were made by several agencies, I succeeded in discovering the snail hosts (Harinasuta et al., 1971; Kitikoon et al., 1973; Sornmani et al., 1973). Unexpectedly, they were not oncomelanid snails as presumed, but members of the genus *Tricula*. *Tricula*, incidentally, has a much different habitat than *Oncomelania*. A colleague, Temcharoen (1971), named the previously undescribed species *Lithoglyphopsis aperta*. In 1976, we (Davis et al.) found that various interpopulation variation occurred in *Lithoglyphopsis* (=*Tricula*) *aperta*, with three main morphological types occurring in Thailand. These we referred to the alpha, beta and gamma races. At the same time, Kitikoon & Schneider (1976) reported that there were another two phenotypes of the gamma race of *L. aperta* found in the southern part of Laos. Since then, *L. aperta* has been transferred to the genus *Tricula* (Davis, 1979). In 1978, Voge et al. distinguished the Southeast Asian schistosome from the more easterly *Schistosoma japonicum* and named it as a new species, *Schistosoma mekongi* Voge, Bruckner & Bruce.

Human schistosomiasis is a complex parasitic disease. It is not easily cured or controlled by any single modern therapeutic means alone. Effective control of this disease is difficult unless, in brief, the epidemiology, ecology, and the biological relationships of the parasite and its molluscan intermediate hosts and its human and reservoir hosts are well understood.

Therefore, my current research is directed toward a better understanding of the pomatiopsid snail *Tricula aperta*. In particular, I wish to know the relationships of the various so-called races of *T. aperta* to each other and their potential for disease transmission in the Laos-Thailand region. This research deals with 1) geographical distribution and habitats of the snails, 2) methods of collecting and handling, development of laboratory culture and maintenance techniques, 3) susceptibility to infection with *Schistosoma mekongi*, 4) cytotaxonomy and 5) genetic variability.

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Lastly, grateful acknowledgement is made for the help and patience of my wife, Prapai Kitikoon, and three children, Pravinee, Kittiyut and Praweena Kitikoon.

GEOGRAPHICAL DISTRIBUTION AND HABITATS

As a result of the extensive field surveys I conducted during the summer months (March to June) of 1972, 1973 and 1974, it was established that the so-called alpha, beta and gamma races of *Tricula* (= *Lithoglyphopsis*) *aperta* were very widely distributed throughout the lower part of the Mekong River in Laos, Thailand and Cambodia, and the Mune River (a tributary of the Mekong) in Thailand (Fig. 1). The alpha and gamma races were found only in the Mekong River, and the beta race only in the Mune River. Even though the extent of the surveys was limited due to political turmoil, lack of security, difficulty of transportation, etc., the distributions of these snails could be estimated to cover at least 200 river miles of the Mekong River. This estimation is based on the two most distant locations where the natural snail host *T. aperta* (gamma race) of *Schistosoma mekongi* is known to occur: upstream at Ban Sabouxai, Savannakhet Province, Laos, and downstream at Sompamit Falls near Ban Khon, southern Laos (near the Laos-Cambodia border) (Fig. 12). It may also be assumed that the gamma race of *T. aperta* occurs additionally at least 100 miles further south to Kratié in Cambodia, because human schistosomiasis has been found in that area. It also is possible to predict that these snails might exist in some areas many miles upstream from Ban Sabouxai, because physiographical and geological conditions of the Mekong River in those regions are very much the same as downstream. However, it is not now possible to search for *T. aperta* in those areas because of the political climate.

These so-called alpha, beta and gamma races of *Tricula aperta* and the related species live in special habitats comprising mainly solid substrates: base sheet rock, or under the bark of dead wood, rocks, shells and other solid materials, including dead leaves of higher aquatic plants (such as those of the shrubby euphorbeaceous rheophytes, *Homonoia* spp., which are quite common along the Mekong and Mune rivers). The *Tricula* snails live neither in mud

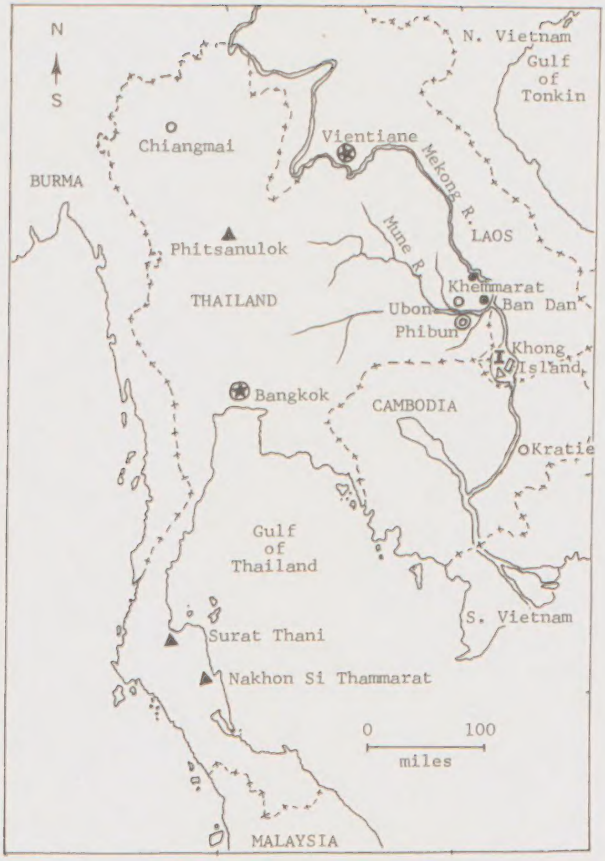

FIG. 1. Map of Thailand and neighboring countries showing foci of human schistosomiasis and known habitats of *Tricula aperta* and related species.

▲= human schistosomiasis - unconfirmed species (possibly *Schistosoma japonicum* or *S. mekongi*); I = human schistosomiasis - *S. mekongi*; for more details see Fig. 12; ● = natural habitats of the alpha and gamma races of *Tricula aperta*; ▯ = natural habitat of the gamma race of *T. aperta* and *Manningiella conica*; for more details see Fig. 12; △ = natural habitat of the gamma race of *T. aperta* and two unnamed taxa of *Tricula*; for more details see Fig. 12; ◎ = natural habitat of the beta race of *T. aperta*; for more details see Fig. 11; – + – + = international boundaries; ⊛ = capital; ○ = province.

nor on algal strands as do other parasite-transmitting snails, but have distinctly different characteristics in regard to habitat and niche preferences. Therefore, habitats of the individual races and very precise geographical locations where these snails can be collected are given below.

The alpha race of *Tricula aperta* (Figs. 2 and 3)

The alpha race of *Tricula aperta*, which is the largest in size in comparison to the other two races, was found only in the Mekong River. The snails live from near the shore out to the center of the river, and they even occur in the stagnant water of shallow pools on the island of rocks in the river. A habitat such as the latter is described later. This island, however, is submerged during the rainy season. The alpha snails of all ages were found underneath stones, normally clustered at the junction of the stone and mud substrate. They preferred to cling to the rocks that were positioned against the water flow. In the shallow pools, they may live in the bark of dead wood. No live snails were found on or in a mud substrate.

Five sites in the Mekong River were found to harbor alpha snails, with varied degrees of abundance. Each of these locations is discussed below.

Ban Sabouxai (site 1) is about 5¼ miles upstream west of Khemmarat, 16°4′N, 105°10′E, Savannakhet Province, Laos (Fig. 9A). The snails live near the shore at depths ranging from less than 1 m to 2 m. The water current in this area is very rapid and the snail population was comparatively low during the period of my observation. It is suspected that the snail population may vary from year to year. Gamma snails also were found in this area and were the dominant species.

Khemmarat (site 2) is at 16°3′N, 105°18′E, Ubon Ratchathani Province, Thailand (Figs. 1, 9B). The snails live off-shore, practically in the center of the Mekong River, where the river bed contains solid substrate (sheet rock), which forms many tiny islands and shallow water passages during the dry season. Here the alpha snails were more abundant than the gamma snails. The best time to collect snails was between the second week of April to not later than the second week of May, when the depth of water was lower than ¾ m; otherwise, the current was too strong.

Ban Bung Kong (site 3) is about 4⅓ miles downstream east of Khemmarat, or about ⅔ mile upstream west of Ban Khi Lek, Khemmarat District, Ubon Ratchathani Province, Thailand (Fig. 9C). This area is different from sites 1 and 2 described above. The rock islands are more numerous and larger, and the water is deeper. Most of the snails cling to the rocks at the edge of the islands facing the center of the river. The gamma snails were abundant and predominant here.

Ban Khi Lek (site 4) is about 5 miles downstream from Khemmarat, 16°2′30″N, 105°18′30″E, Khemmarat District, Ubon Ratchathani Province, Thailand (Fig. 9D,E). The alpha snails were found in the shallow pools situated on the largest rock island in this area (Fig. 9E). This island was formed by rock out-crops which extend from Ban Bung Kong less than a mile from the west of Ban Khi Lek. The island is submerged during the rainy season. There were some aquatic plants growing on the island and around the edge of the pools. The bottom of the pools is composed of sheet rock covered with silty soil from sedimentation during the flood period. The alpha snails were abundant; other snails were few. No snails of the gamma race of *Tricula aperta* were found in these pools. It needs to be stated here that the shell morphology of the alpha snails from these pools (Fig. 3) is quite distinct from alpha snails from other locations (Fig. 2). Their shells were oblong and slender, whereas the shells of other populations of alpha snails were rounder and shorter. These two alpha shell types may represent sibling species.

Ban Dan (site 5) is located about 90 river miles downstream south of Khemmarat, 15°19′15″N, 105°30′45″E, Ban Dan District, Ubon Ratchathani Province, Thailand (Figs. 1, 10). The alpha snails live at the edge of a large island in the middle of the Mekong River, a few hundred meters from the mouth of the Mune River. This locality is technically in Laos according to the treaties of 1893 and 1926, which awarded the largest islands in the Mekong River to Laos. Therefore, this area can be referred to Vapikhamthong Province, Laos. Both alpha and gamma snails were found in approximately equal numbers during my observations. Beta snails also were suspected to exist in this area, but an extensive search has never been made for them. Fewer alpha and gamma snails were observed at this location in comparison with the other four sites (no gamma snails were found in the pools at the fourth site). No attempts were made to observe alpha snails downstream beyond this point. However, gamma snails were abundant at Khong Island and the adjacent areas about 120 miles further downstream, but not a single alpha snail was found in these areas. Therefore, alpha snails were assumed to exist between its southernmost location at Ban Dan, Ban Dan District, Ubon Ratchathani Province, Thailand, and upstream at Ban Sabouxai, Savannakhet Province, Laos (site 1), or many miles northward beyond this point as mentioned previously.

FIGS. 2-8. Shells of *Tricula aperta* and related species. FIG. 2. *T. aperta*, alpha race (river form). FIG. 3. *T. aperta*, alpha race (pool form). FIG. 4. *T. aperta*, beta race. FIG. 5. *T. aperta*, gamma race (the natural snail intermediate host of *Schistosoma mekongi* at Khong Island, Sithandone Province, Laos). FIG. 6. A non-pigmented form, a phenotype (or possibly a distinct species or sibling race) of *T. aperta*. FIG. 7. A pigmented form, another phenotype (possibly a distinct species or sibling race) of *T. aperta*. FIG. 8. *Manningiella conica* or possibly *"Tricula" conica*.

Scale lines are divided into millimeters. Scale A is for Fig. 2; Scale B is for Figs. 3-8.

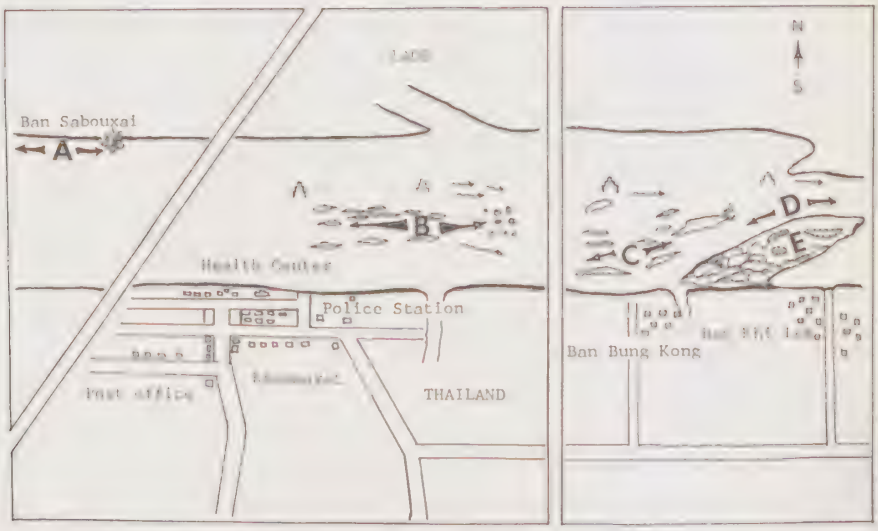

FIG. 9. Map of the Mekong River at Khemmarat and adjacent areas. A, Ban Sabouxai, about 5½ miles west of Khemmarat; the gamma race was predominant here. B, Khemmarat, about 1⅓ miles east of the market place; this area was inhabited markedly by the alpha race (river form) of *Tricula aperta*. C, Ban Bung Kong, about 4⅓ miles downstream east of Khemmarat; the gamma race was predominant here. D, Edge of the largest island facing the middle of the river, rapid water flow, Ban Khi Lek ⅔ mile east of Ban Bung Kong; the gamma snails were predominant here. E, Pools on the largest rocky island (same as D) in front of Ban Khi Lek; the alpha snails (pool form) were predominant here.
= island; = rough current; = pool on rocky island; = French channel marker; = bushes; = housing; = sheet rock; = road.

The beta race of *Tricula aperta* (Fig. 4)

The beta snails were found to occur only in the Mune River, at Phibun Mangsahan, 15° 14′ to 14′45″N, 105°17′15″ to 30″E, Ubon Ratchathani Province, Thailand (Figs. 1, 11). The Mune River is a tributary of the Mekong River. These snails preferred to live near shore on the solid substrates around shrubby areas. Here the water current was comparatively fast. The beta snails cling to the rocks in the same manner as the alpha snails, but the beta snails were not found in pools or in stagnant water. They usually were abundant beneath the rocks, inside the loose bark of dead wood and on other solid substrates such as shells and twigs. The distribution of the beta snails ranged from a few meters upstream from Kaeng ("white rapid current") Sa-Pŏe (site 6) (Fig. 11A,B), a tourist area near the Phibun business area, to downstream, east to the left bank at Kaeng Kao (site 7) (Fig. 11C) and at Kaeng Kum-Poung (site 8) (Fig. 11D,E) on both the right bank (around the bushes near the boat passage where the current was very swift) and the left bank (around the bushes near shore about 300 m above the water passage).

The gamma race of *Tricula aperta* (Fig. 5)

The gamma snails have a greater distributional range than the other two races of *Tricula aperta*. They were found only in the Mekong River, ranging from upstream at Ban Sabouxai on the Laotian side down to Sompamit Falls near Ban Khon in Laos, close to the Laos-Cambodia border. As mentioned previously, they may exist many miles upstream beyond Ban Sabouxai and about 100 miles downstream from Ban Khon to Kratié in Cambodia. Therefore, the total range of distribution of the gamma snail in the Mekong River is over 300 miles and includes three countries, Cambodia, Laos and Thailand. In many areas, the gamma snails shared habitats with alpha snails.

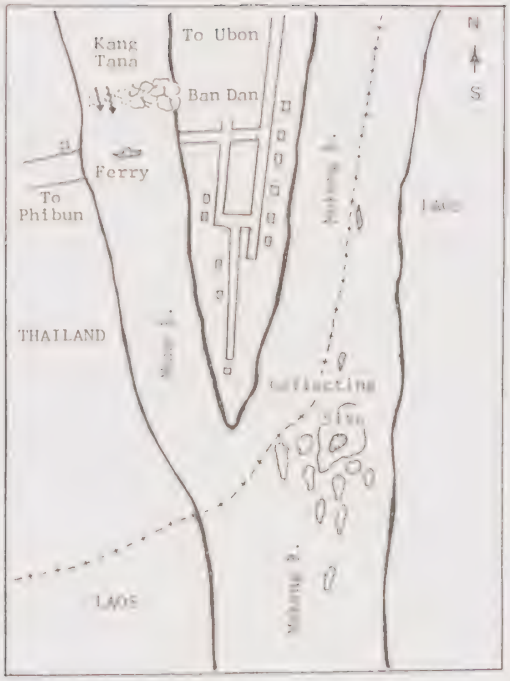

FIG. 10. Map of the Mekong River at Ban Dan, showing the collection site (almost in Laos) of the alpha and gamma races of *Tricula aperta*.
= sheet rock; = small pool on a rocky island; = small island; = rough current; —+—+— = international boundaries; □ = housing.

Maturation periods and shell morphology were very diverse in the gamma snails found in the southern part of Laos at Khong Island and adjacent areas (close to shore above Sompamit Falls near Ban Khon) and in the northeast of Thailand at Khemmarat and nearby areas. The maturation of the gamma snails at Khong Island usually started as early as the third week of April and the snails appeared fully mature by the middle of May annually, whereas at this time in the Khemmarat area these snails were still very young.

The morphology of shells of the gamma snails found at Sompamit Falls was somewhat atypical. At this locality, two additional phenotypes (perhaps sibling races or possibly new species) were observed. The first phenotype contained no tiger-stripe color pattern on the mantle of the body whorl. The shape of the shell was similar to that of the gamma race found elsewhere, but the shell was somewhat smaller (Fig. 6). The second phenotype had a more depressed shell with a wider aperture and a slightly reflected lip. The body whorl was also rounder and the apex shorter. The pigment patterns on the mantle of the body whorl were very similar to those of the gamma race (Fig. 7).

The characteristic habits of the gamma snails were somewhat intermediate between those of the alpha and beta race. The gamma snails preferred to live in clean and clear water with very high oxygen content (Kitikoon & Schneider, 1976), e.g., water that was very swift (either shallow or deep, i.e., depths ranging from a few centimeters to many meters at the bottom of the center of the river). However, they also could inhabit water that was almost stagnant. The gamma snails lived mostly on rocks, twigs and inside curled dead leaves. However, when gamma snails were very young, they tended to live beneath rocks near the junction where the rocks rest on silty soil substrates. Thirteen accessible sites were observed for gamma populations (Figs. 1, 9, 10, 12). The first five sites, i.e., Ban Sabouxai, Khemmarat,

FIG. 11. Map of the Mune River at Phibun Mangasahan, showing five habitats of the beta race of *Tricula aperta*. A,B, Kaeng Sa-Pŏe, tourist and bathing areas; A was above the rapids and B was below the rapids; in these two areas, the numbers of beta snails were comparatively small. C, Kaeng Kao, on the left bank of the Mune River opposite Ban Hin Laht; the numbers of snails here were comparatively large. D,E, Kaeng Kum-Poung; D was at the left bank and comparatively high numbers of beta snails were found here; E was near the boat passage, where the water was rapid and the numbers of beta snails were high.

= island; = rapid current; = sheet rock; = bushes; = pool.

Ban Bung Kong, Ban Khi Lek and Ban Dan, were described previously. Although the fourth site at Ban Khi Lek had hardly any gamma snails in the pools (Fig. 9E), the snails were abundant at the edge of the island which faced the center of the river (Fig. 9D).

The other eight sites where gamma snails were found were at Khong Island and the adjacent areas, Sithandone Province, southern Laos (Fig. 12). These locations were: Ban Vern Thong, Ban Xieng Wang, Thomas Dooley Foundation Hospital (= Moung Khong Hospital), Ban Na, Ban Hin Siou, Ban Hat Sai Khoune, Papaeng Falls and Sompamit Falls. These sites are discussed in more detail below.

Ban Vern Thong (site 9) is located upstream about 2 miles north of Khong Town on the east shore of Khong Island (Fig. 12). Here the gamma snails were comparatively few.

Ban Xieng Wang (site 10), Thomas Dooley Foundation Hospital (site 11) and Ban Na (site 12) were situated on the southeast shore of Khong Island between the northern and southern borders of Khong Town; 14°6′-7′30″N, 105°51′-51′45″E; Sithandone Province, southern Laos (Figs. 1, 12). The gamma snails were the most abundant in these three locations. In addition, a sibling species of *Tricula aperta*, named *Manningiella conica* Temcharoen 1971, was numerous near the shore just in front of the Thomas Dooley Foundation Hospital. These *M. conica* snails were found mostly on twigs with the gamma snails. More details will be discussed later. The natural transmission site of *Schistosoma mekongi* exists near the shore of Ban Xieng Wang (Kitikoon et al., 1973) (Fig. 12). Therefore, snail collecting in these areas must be done with great caution, especially during the summer months (late March through early June).

Ban Hin Siou (site 13) is situated at the southwestern shore near the southernmost tip of Khong Island (Fig. 12). Very few gamma snails were found here.

Ban Hat Sai Khoune (site 14) is a small village situated on the mainland at the right bank of the Mekong River just opposite Ban Xieng Wang (Fig. 12). The number of gamma snails here was low.

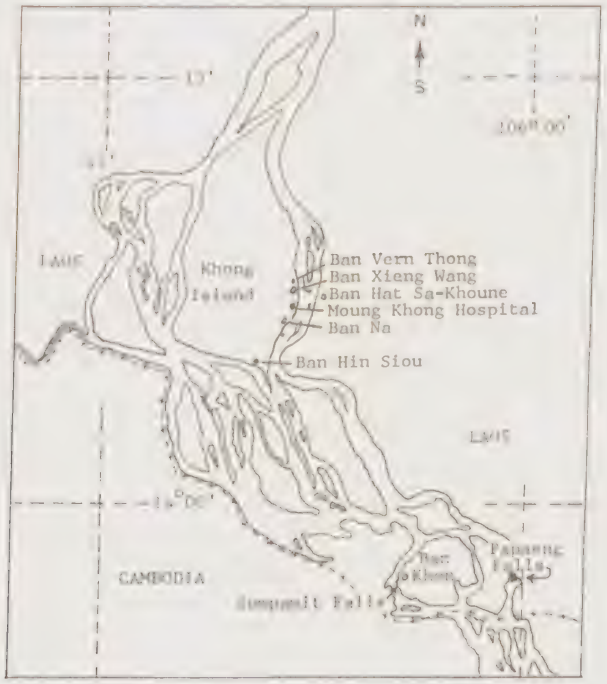

FIG. 12. Map of the Mekong River at Khong Island and adjacent areas, showing eight collection sites for the gamma race of *Tricula aperta*, two other phenotypes of *Tricula* (at Sompamit Falls) and *Manningiella* (= ? *Tricula*) *conica* at Moung Khong Hospital.

Papaeng Falls (site 15) are the largest water falls formed by the Mekong River. Their location is 13°56′N, 105°59′E, Sithandone Province, southern Laos (Fig. 12). The gamma snails existed near the shore on the right side of the Mekong River both above and below the falls. No attempt to collect snails on the opposite side of the falls was made.

Sompamit Falls (site 16) are about 1½ miles southwest of Ban Khon and about 2 miles from the Laos-Cambodia border, 13°57′30″N, 105°55′E, in Sithandone Province, southern Laos (Fig. 12). The water in this area was comparatively shallow (except for the main water passage which went directly to the falls); it was considered to be a swamp, because the water was shallow and it had dense stands of various kinds of aquatic plants. Most of the snails were found under shade in slow running water. The gamma snails, and presumably the other phenotypes as well, were numerous in this area. They were all sympatric, living on rocks or twigs. They seemed to mature at the same time.

An additional species, *Manningiella conica*, which existed in the Mekong River near the shore in front of the Thomas Dooley Foundation Hospital, Khong Island (Fig. 12), should be described, since these snails were also susceptible to *Schistosoma mekongi* (see Kitikoon, 1981). These snails looked very similar to the gamma snails, except that they had conic spires, their shell shape was slightly slenderer, and the shell height was greater (Fig. 8). I have always considered *M. conica* to be a sibling species (or possibly sibling race) of the gamma snails. Likewise, Davis (1979) abolished the genus *Manningiella* and transferred all species except *conica* to other genera. Due to the time of maturation of gametes, and radular and pigment characteristics, Davis suspected *M. conica* to be related to *Tricula*. Unfortunately, no one has been able to collect these snails in order to repeat the studies because of international political turmoil present in the area. Therefore, a number of questions which have been raised (e.g., is *M. conica* the same race as the gamma snails, since they were susceptible to the Mekong schistosome in the laboratory and the morphology of the two species is very similar?) must be deferred for the present.

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STUDIES ON *TRICULA APERTA* AND RELATED TAXA, THE SNAIL INTERMEDIATE HOSTS OF *SCHISTOSOMA MEKONGI*. II. METHODS FOR COLLECTING, HANDLING, CULTURING AND MAINTENANCE

Viroj Kitikoon

ABSTRACT

Tricula aperta is found in Thailand, Laos and Cambodia in the Mekong and Mune rivers on submerged solid substrates. To collect the snails, a hand-picking technique was found to be the best. The snails are very sensitive to environmental change and many die during transportation. Only sorted healthy and clean snails were satisfactory for transporting. Small glass or plastic bottles with air tight lids and plastic thermos bottles were found to be excellent for transportation, but they must contain washed rocks and conditioned water. Diatoms should be added 4-5 days prior to adding the snails to establish diatom colonies. Water in the container must be aerated periodically.

Raising the snails to maximum size in the laboratory was quite difficult. Although small bottles and crystallizing dish vivaria were successful, a prototype stream aquarium was found to be one of the best ways to raise the snails. Medium organic-rich mud, small rocks and diatoms are essential for culturing and maintaining these snails.

COLLECTING AND HANDLING METHODS

Introduction

Many workers have experienced difficulties in collecting and transporting live alpha, beta and gamma races of *Tricula aperta* (Temcharoen) to the laboratory. The difficulties in collecting were due to the diverse habitats of the three races and the habits of the snails, which necessitated new collecting and handling methods. Conventional scooping or sieving techniques will not work for these snails because they do not live in mud or on algal strands or float in water as do many other vector snails. The conventional methods of preparing snails for transportation by simply wrapping them with moist paper or by keeping them in a container with water will not work very well either. Most snails die during transportation when such methods are used, because the crowded conditions cause deterioration of water, which leads to suffocation of the snails. I have succeeded in collecting and transporting a large quantity of these snails from the field to the laboratory by using the following procedures.

Snail collecting technique

Since the snails are very small and cling onto hard substrates in various depths of water, a hand-picking technique is the most appropriate way to collect them. The collector, of course, must work in the water or even dive to remove the substrates from the water prior to harvesting the snails from them (Figs. 1-6). One important aspect must be kept in mind – avoid getting infected with schistosome cercariae while collecting the snails. Therefore, in areas where infection occurs, precautions must be taken to prevent direct water contact. Areas which have already proven to be endemic for schistosomiasis mekongi are Khong Island and adjacent areas (Figs. 7-9) (Barbier, 1966; Kitikoon, 1970; Iijima et al., 1971; Sornmani et al., 1971; Harinasuta et al., 1972). Moreover, Kitikoon et al. (1973) found that Ban Xieng Wang in Khong Town is a natural transmission site of *Schistosoma mekongi* Voge, Bruckner & Bruce by the gamma snails. Normally, collecting is safe if thick rubber gloves (mid-arm

FIGS. 1-3. Collection sites in the Mekong River for *Tricula aperta*. FIG. 1. Site for the gamma race, near shore at Ban Sabouxai (Laotian side); arrow indicates Thai side. FIG. 2. Site at Ban Bung Kong, facing Laos; the gamma race was abundant here, as indicated by arrows. FIG. 3. A pool on the largest rocky island at Ban Khi Lek; the alpha race (pool form) was abundant here. Arrow indicates an aquatic plant, *Homonoia* sp.

FIGS. 4-6. Collection sites for *Tricula aperta*. FIG. 4. Site at Ban Dan, near the edge of the largest island in this area in the Mekong River; arrow indicates Laos side. FIG. 5. Diving for alpha and gamma snails off rocky island at Ban Dan, in Laotian part of the Mekong River; arrow indicates a small rock bearing snails. FIG. 6. Rapids at Kaeng Sa-Pöe, Mune River at Phibun Mangsahan; black and white arrows indicate sites where beta snails were collected.

FIG. 7. Aerial view of Khong Town (= Moung Khong), Khong Island, showing transmission site of *Schistosoma mekongi* (white arrow); black arrow indicates the mainland of the right bank of the Mekong River, Laos. FIG. 8. Transmission site of *S. mekongi* at Ban Xieng Wang, Khong Town; arrow indicates bushes of *Homonoia* sp., which served as a defecating area for inhabitants. FIG. 9. Collection of snails at the principal collecting site at Ban Xieng Wang, illustrating precautions (rubber gloves and boots); arrow indicates small rock, bearing snails. For more details, see Figs. 10-12.

FIGS. 10-12. Habitats of young snails of the gamma race of *Tricula aperta*. FIG. 10. A rock, with forceps and arrows pointing at very young gamma snails. FIG. 11. Arrows indicate very young gamma snails inside a curling leaf. FIG. 12. Arrows indicate very immature gamma snails on a submerged twig. Note: size of thumb indicates the relative sizes of the rock, leaf, twig and snails.

length) and rubber boots (knee length) are worn (Fig. 9). Concentrated ethanol or methanol is useful for sterilizing the body surface if there is accidental contact with contaminated water. In many collection sites, the only way to collect the substrates is by diving (Fig. 5). The size of rocks with snails varied from those smaller than a child's fist (Figs. 5, 9, 10) and weighing less than a quarter of a pound to as heavy as many pounds.

Care must be taken when harvesting the snails from their substrates (Figs. 10-12). Their shells are very small (less than 2 mm) and fragile, especially when they are immature. Cracking of some shells during collection often occurred, particularly when the snails were scraped from the substrates. The snails with cracked shells will soon die and cause a problem during temporary storage in the field and during transportation to the laboratory. Preventing damage to the shells during harvest is quite easy if snails on the substrates are exposed to air or direct sunlight for a few minutes prior to washing into a container. The container (a plastic bucket is preferable) should be three-fourths filled with water. If some snails were still left on the substrates, especially between cracks in the rocks or in the fissures of bark, a small piece of wood or a hard bristle brush could be used to carefully scrape off the snails. A pair of forceps grasped gently also could be used for picking off snails individually.

Snail preparation for handling and shipping

Two steps are needed in this procedure: cleaning and sorting.

Cleaning

Cleaning the snails is one of the most important steps in preparing snails prior to their transportation. Most snails collected from the field are contaminated with mud, aquatic macro- or microorganisms, fermented organic compounds, etc., which can initiate putrefaction or fermentation in the water. Putrefaction of dead organisms and fermentation of some materials deteriorates the quality of water and causes the snails to die from suffocation. Cleaning the snails can be performed in two ways: a) by washing the snails in a bucket by gently stirring them with one's hand (wearing gloves in case the snails should be infected) and changing the water repeatedly until the water is clear; or b) by washing the snails in a sieve; this can be done in the river or pool. The latter is considered a better method because the snails can be cleaned more quickly, more efficiently and with less damage to them. However, the sieving must be done with great care or the snails may be washed away by the current if the water is swift. Washing is done by shaking the sieve or stirring the snails in the water. Large pieces of debris, which may not go through the holes of the sieve, can be removed by hand or by quickly dipping the sieve vertically into the water and slowly moving it horizontally away from the debris about 3-5 inches below the surface of the water. This procedure can be used in stagnant or very slowly running water. The procedure may be repeated if necessary.

Sorting

Two important aspects should be remembered in sorting snails: separate only the species wanted and screen for healthy snails. Only healthy snails which can survive the hardships of transportation should be kept. Many snails may be injured, making them weak or resulting in their deaths during field collection. Screening for healthy snails while in the field or in a temporary laboratory is not difficult, since we know that these snails prefer to cling to the rocks. Active and healthy snails can be trapped by simply adding well-washed rocks into the vessels (plastic buckets, plastic or enamel pans) containing snails. The snails will move to and attach themselves to the rocks, and can thereby be trapped. These snails then can be transferred to other containers. Some of the healthy snails may cling to the sides or to the bottom of the vessel. They may be separated from the weak or dead ones simply by discarding

some water and slowly swirling the container for a few seconds. The weak and dead snails remain loose and accumulate at a certain part of the container (the container could be slanted while swirling). The water containing these snails is then suddenly poured into another container. A few healthy snails may possibly be taken away by this action. Therefore, the procedure may be repeated if desired. In any procedure, the snails must be allowed to move freely for at least 30 min in the undisturbed container prior to going on to the next steps.

Container preparation

Container selection and preparation is one of the most important aspects in transporting snails alive to the laboratory. The type of container used normally depends on the number of snails and the type and duration of transportation. There are no differences in results if the containers used are prevented from being broken during shipment. However, I found three types of containers to be very useful for carrying and transporting snails from remote field areas (e.g., Ubon Ratchathani Province, Thailand, and Khong Island, Sithandone Province, Laos) to the laboratory in Bangkok, Thailand, and to the laboratory in the Mollusk Division, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A. Less than 1% of the snails died during transportation. These containers were as follows.

1. A plastic bucket of about 5 U.S. gallon capacity with a water-tight lid. This type of container was best for carrying a large quantity of snails for a short trip.
2. A foam-insulated plastic thermos of about 1 U.S. gallon capacity. This was an excellent container for carrying a medium quantity of snails (about 2,000 to 3,000 snails per container, depending on the length of the trip). Its advantages were in being unbreakable and in maintaining a constant water temperature, thereby stabilizing the water conditions. Moreover, the size was not too large for hand carrying and was very appropriate for carrying during air travel.
3. Glass bottles about 3 inches in diameter and 4 inches in height with water-tight lids. These were found to be the best containers for keeping various species separate while being transported at one time. They were also very convenient if it were necessary to change the water. Also, dead snails were easily seen and removed prior to their deteriorating the water. If any one of the bottles turned bad and all the snails died, then the snails from the other bottles were still left for study, because many bottles could be carried at the same time. The only disadvantage is the danger of bottle breakage, but this could be avoided by using hard and clear plastic bottles.

Preparing the containers for transporting the snails was normally not very complicated. Triculine snails are gill-breathing operculates which live in water saturated with dissolved oxygen. They were very sensitive to environmental changes, especially when kept in a confined area during transportation. Under the latter conditions, they withdrew the head and foot into the shell and closed the shell aperture very tightly with the operculum. They dropped to the bottom of the container and rolled around due to turbulence of the water caused by the moving vehicle. Snails disturbed in this way would not come out from their shells and would soon die from suffocation within their shells, even though the water quality had not yet been altered. When such snails began to die, natural autolysis promoted bacterial growth, which initiated putrefaction and fermentation. Since the climate in their native regions is hot, putrefaction and fermentation occurred very rapidly. Polluted conditions within the containers then follow, which was another factor causing all snails in that container to die.

These problems were eliminated, or at least controlled, by adding clean rocks or stones to the container and increasing the aeration of the water. The size of the rocks used varied directly with the size of the containers. The water was aerated periodically. The rocks in

the container helped prevent turbulence of the water and provided additional shelter and surface areas for the snails. Also, the rocks protected the snails from rolling, because the flat area at the bottom of the container was limited. Using rocks collected from the field also provided some natural foods, i.e., diatoms and other food items, for the snails during transportation. In addition, aeration from a small air-pump provided dissolved oxygen to stabilize water conditions in the container. When the physical problems were eliminated and the biochemical changes reduced, the water conditions were stable or were altered only very slowly. Therefore, the snails could be kept in the container for a longer time, and the container was suitable for handling and shipping.

Procedures for container preparation were: 1) the rocks used were selected from the ones which were found to have an abundance of snails; 2) the rocks were well washed (but not scrubbed with hard brushes) prior to use (the sizes of rocks varied according to the size of containers); 3) the containers were washed (not with detergent) prior to use; 4) the rocks were well fixed and free from movement in the containers, but were arranged to give enough room between them for the snails to cling. The amount of rocks used depended on the type of containers. I filled the plastic buckets only three-fourths full of rocks to prevent breakage, but I put in rocks almost to the mouth in the plastic thermos and the small glass bottles. My purpose was to have enough room to keep a plastic tube coiled in the container's neck when the tube was not in use. If the rocks projected above the mouth of the containers, the lid could not be used. An air stone, connected to a plastic tube, was placed in the bottom of the container prior to adding the rocks. The air tube was connected to an air-pump operated by dry cell batteries (A/C current also can be used depending on availability). Conditioned water was added prior to adding the snails. River water was especially good to use. The snails' food and some trace substrates were added. I prepared these containers for 4-5 days prior to use and kept them under artificial sunlight (fluorescent lamp) in order to observe the water conditions and allow the diatoms to grow.

I have used this method of container preparation for hand carrying the alpha, beta and gamma races of *Tricula aperta*, as well as *Lacunopsis* and *Hubendickia* spp., from the Mekong and Mune rivers in Ubon Ratchathani Province, Thailand, to the laboratory at The University of Michigan, a five-day trip. The death rate of the snails during several such trips was less than 1%.

CULTURE AND MAINTENANCE

Introduction

All specimens used for various aspects of this study were from young field-collected snails. They were too small for use in some of the experiments and therefore had to be maintained and cultured in the laboratory to allow them to grow and mature. Also, some experimental snails had to be kept in constant good condition during observations. Therefore, it was necessary to have a reliable maintenance method. Various culturing and rearing methods for *Tricula aperta* have been established for some time, ever since this snail was shown to be the intermediate host of *Schistosoma mekongi*. However, most methods had the same disadvantages, i.e., they were not dependable, were not efficient for mass maintenance and production of young, or were too complicated, etc.

Liang & van der Schalie (1975) developed a culture method using Petri dish vivaria for the gamma race of *Tricula aperta*; their method could be used also for the alpha and beta races. Their procedure was quite complicated and therefore not practical. In 1976, Liang and Kitikoon modified Liang & van der Schalie's method, obtaining better results (Liang & Kitikoon, 1980). However, this latter method was suitable only for a small number of individuals in each culture colony. In 1976, Lohachit et al. (1980) began developing a method for culture

and maintenance of *T. aperta* using Petri dish and bottle cultures to which were fed diatoms. They found that the bottle cultures were more productive and more suitable for the development of baby snails. A mass production technique, however, had not yet been obtained.

Culture and maintenance of the three races of *Tricula aperta* used during this study followed the methods of Liang & van der Schalie (1975), Liang & Kitikoon (1980) and Lohachit et al. (pers. comm., 1976; 1980), with some minor modifications, mostly in the type of vivaria and snail food.

An artificial stream aquarium was one of the most interesting types of culture container employed in the current study. This method was devised in order to simulate a natural snail habitat in the laboratory. Some of the results indicated that this culturing method probably would be one of the best for *Tricula aperta* mass production, if some technical problems could be eliminated. Details of my study and observations follow.

Materials and methods

Snails

All snails used during the study were field collected from three localities. The alpha snails were collected from a pool on the largest rocky island in the Mekong River in front of Ban Khi Lek (Fig. 3), the beta race was from the Mune River at Kaeng Kao, and the gamma race of *Tricula aperta* was from the Mekong River at Ban Bung Kong (Fig. 2).

Food and food additives

Four types of food and food additives were used for feeding the snails during the study. They are as follows.

A. Diatoms. *Navicula pelliculosa* (University of Texas culture no. 688) and *Achnanthes exigua* var. *agterovalva* were used as a major food supply throughout the study. *A. exigua* was isolated from a rock from the Mekong River.

A 2.8 liter culturing flask (Fig. 13) was used for establishing the diatom colonies under cool fluorescent light at 22-25°C. The culture medium (Table 1) followed Guillard (1975), with some minor modifications, i.e., adding soil extract, alfalfa extract and coarse sand granules. The soil extract was prepared by using about 300 g dry weight of soil (see Substrate, below) in 1 liter of tap water and autoclaved at 15 lb/square inch pressure or approximately 240°F for 1 hr. After autoclaving, the soil was allowed to settle (in a refrigerator). About 25 ml of the clear supernatant was used to make 1 liter of the culture medium. The alfalfa extract was prepared in the same way as the soil extract, but only about 50 g of dry weight alfalfa was used. The volume of alfalfa extract used in the culture medium was the same as that for the soil extract (25 ml). The medium could be prepared in a large amount at one time and kept sterile in the refrigerator.

Each new set-up was autoclaved prior to inoculation with the seed diatoms from the stock culture. One cup of sand was added to the culture prior to sterilization. Sand provided more surface area in the culture flask for the diatoms to grow and it also aided in loosening the diatoms from the side of the culturing container when the diatoms were collected. The diatoms were collected by simply swirling the contents of the culture flask. The diatoms were thereby loosened from the sand, and the swirling sand scraped the diatoms from the sides of the culture flask, the diatoms then becoming mixed with the culture medium. The culture medium (with diatoms) was then poured into a funnel flask under sterile conditions using a hot flame to prevent contamination inside the culture flask. By this means, the culture could be recycled many times. This procedure was found to be very successful during my study, both for saving time and for excellent mass production of diatoms.

Any culture contaminated with green algae, fungi, etc., had to be discarded and the whole

TABLE 1. Composition of the stock solution used to culture *Achnanthes exigua* var. *agterovalva* and *Navicula pelliculosa*.

Nutrient elements and extract solution	Stock solution (g/l)	Stock solution used in final medium (ml/l)
$CaCl_2.2H_2O$	36.76	1
$MgSO_4.7H_2O$	36.97	1
$NaHCO_3$	12.60	1
K_2HPO_4	8.71	1
$NaNO_3$	85.01	1
$Na_2SI_3.9H_2O$	28.42	1
H_3BO_3	0.6% (wt/vol)	1
Soil extract*	300 g dry weight	25
Alfalfa extract	50 g dry weight	25

*Soil extract rich in organic matter is preferable.

procedure restarted. The collected diatoms were washed two or three times, using conditioned water, prior to feeding the snails, in order to remove any possible toxic elements from the culture medium. Prepared diatoms were then added to the snail cultures two or three times a week. The amount used varied according to the size of the vivaria and the number of snails. The culturing time used was approximately 12 days for the most satisfactory results.

B. Microalgae. *Nostoc muscorum*, a blue-green algae, was used for culturing the alpha race of *Tricula aperta*. The method of preparation followed Liang (1974).

C. Mineral and vitamin supplements. Multivitamins, vitamin B complex, vitamin E and calcium carbonate were tried. Pre-testing for the amount of supplements to use with each culture was always performed prior to the culture experiments.

D. Leaves and filter paper. Dry ground maple leaves and filter paper were used as food additives. The maple leaves were boiled or autoclaved for half an hour and washed prior to being dried and ground.

Substrate

Mud from the habitat of *Pomatiopsis cincinnatiensis*, described by van der Schalie & Davis (1965), was used as a substrate, as well as for soil extract and for culturing *Nostoc muscorum*. The method of sterilization followed van der Schalie & Davis (1965).

Water

Tap water was used for both diatoms and snail cultures. Hot tap water from a storage tank in the Museum of Zoology, The University of Michigan, was conditioned by adding a sodium thiosulphate solution (5% solution, 1 ml/10 gal) and aerating for 48 hrs prior to use in snail cultures. For diatom cultures, the water could be used either hot or cold directly from the tap. No differences were found in using distilled water or tap water from the Ann Arbor city water supply. Using the latter was more convenient and saved time. The amount of water used varied according to the size of the container, but, in general, it filled three-fourths to four-fifths of each container.

FIGS. 13-15. Diatom cultures and maintenance of *Tricula aperta*. FIG. 13. Arrows indicate the diatom culture set-up; the second shelf at the right contains small bottle cultures of *T. aperta*; the third shelf at the right contains crystallizing dish cultures. FIG. 14. Close-up view of a crystallizing dish culture. FIG. 15. Glass tank cultures.

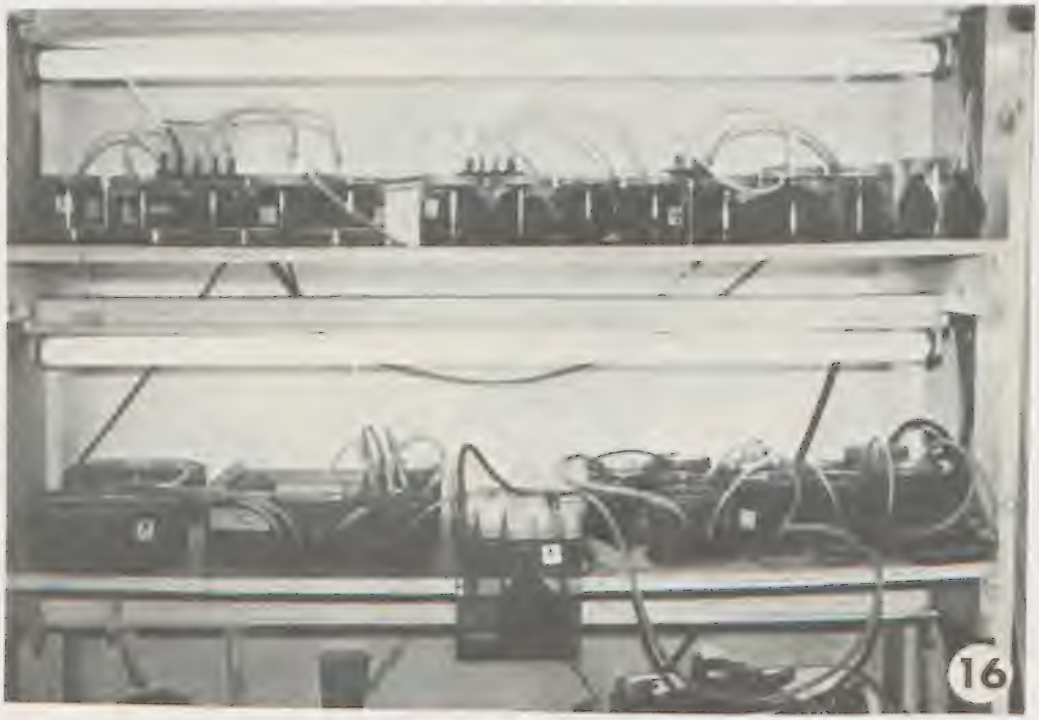

FIG. 16. Small bottle and crystallizing dish cultures, showing aeration set-up. FIG. 17. Modified type of artificial stream aquaria set-up.

Light

White-cool-fluorescent lights were used at 12-hr photoperiods for snail cultures and were considered as a constant factor. Continuous 24-hr light was used for diatom culture.

Temperature

The water temperature used during the study ranged from 22-28°C.

Types of aquaria

Five types of aquaria were employed, as follows.

A. Crystallizing dishes (Figs. 13, 14, 16). Three sizes were used: 9 cm in diameter and 5 cm in height; 12.5 cm in diameter and 6.5 cm in height; and 18 cm in diameter and 9 cm in height.

B. Petri dishes, 9 cm in diameter and 2 cm in height.

C. Bottles (Figs. 13, 16), 8.5 cm in diameter and 9.5 cm in height.

D. Glass aquaria (Fig. 15). Two sizes were used: 24 x 36 x 28 cm and 27 x 51 x 31 cm in width, length and height, respectively.

E. Artificial stream aquaria (continuous flow, closed system). Two types of containers were used: a prototype or a small artificial stream aquarium and a modified or medium-sized artificial stream aquarium. The details are listed below.

1. *The prototype artificial stream aquarium.* This was a small stream aquarium 26 x 34 x 9 cm in size (Fig. 18). The aquarium was made from transparent plastic. Inside, the container was divided into six small passages by five plastic septa (4.5 x 30 cm) to form a canal (Fig. 18A). Two holes were located at different positions in one end (Fig. 18B). The lower hole was a water outlet and the upper one was a water inlet. These two holes were connected with each other by a rubber tube which ran through a filter jar (Fig. 18C). The rubber tube which connected the water inlet and the bottom of the water jar also connected to an air tube from a central air pump. Pressure from the air pump drove water out from the tube to the aquarium, giving a low water level in the filter jar. Thus, water flowed from the culture container to the filter jar through the water outlet. By this action, water continued to flow as long as the pressure in the air passage was maintained. The rate of the flow was about 15 ml/second.

Prior to culturing, the culture container was cleaned and prepared by making a mud mound on the bottom and adding some small rocks to simulate the natural habitat. Mud and rocks were sterilized prior to use. Sterilized water was then added and inoculated with *Nostoc muscorum* (this method was used prior to establishment of the diatom culture). The whole aquarium set-up was placed under artificial light for 10-14 days to allow *N. muscorum* to grow. The aquarium was then readied for use by simply draining off the water and replacing it with conditioned water. Any overgrowth of *N. muscorum* was removed. Snails were added to the apparatus to start the operation. This container could carry 400-500 snails for maintenance and about 100-200 snails for breeding. The optimum number of snails for this system, however, is still not known. The water level in the container was always kept above the level of the water outlet.

2. *The modified type of artificial stream aquarium* (Figs. 17, 19). The function of this type of artificial stream aquarium was the same as the above model, but the components of the culture were slightly different because this model was basically larger. It consisted of five important components: main stream container(s), water storage(s), water pump, water pipes (PVC pipes = polyvinyl chloride pipes) and drain passage.

a. Main stream container(s). This was the main part of the aquarium which was used for culturing or maintaining snails. Its inside dimensions were approximately 33.5 x 51 x 7.5

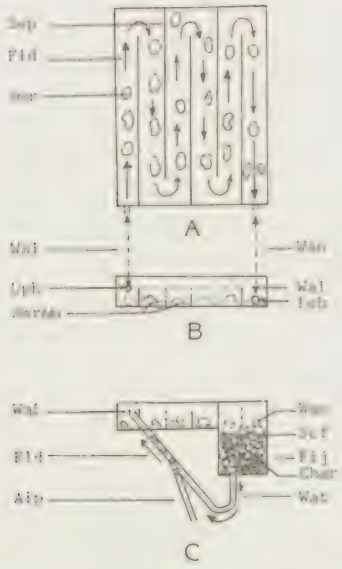

FIG. 18. Diagram of a prototype of the artificial stream aquarium. **A**, top view. **B**, Front view. **C**, front view when connected to a filter jar.

Abbreviations: Aip = air passage; Char = charcoal; Fij = filter jar; Fld = flow direction; Loh = lower hole; Scf = synthetic cotton filament; Sep = septum; Smr = small rock; Smr&m = small rock and mud; Uph = upper hole; Wai = water inlet; Wal = water level; Wao = water outlet; Wat = water tube.

cm, and it was made of plexiglass (3/16 inch thick). The inside of the container was divided into four longitudinal incomplete compartments of equal size by using three pieces of plexiglass (7 x 44 cm) glued together with waterproof cement. This formed the trough for the artificial stream. The stream was about 224 cm long, 7.8 cm wide, and the water was about 7 cm deep. A valve at the water outlet was used for regulating the water level in the stream during the operation. The water outlet was located about 4.5 cm above the bottom of the container. Thus, the water could not totally drain away in the event that the system was shut off accidentally. The total volume of water in the stream during the flow operation was approximately 9 liters, and was 5 liters when the circulating mechanism was shut off.

The main container was connected to a water pump by a PVC pipe (3/4 inch in diameter at the pump and adapted to 1/2 inch diameter at its other end, which was the water inlet of the main container) and connected to the water storage tank by a wooden drain. When the whole unit was engaged, the water circulated from the water storage through the water pump to the culture container, flowed in the artificial stream, and drained back to the tank through the drain passage. Therefore, this was a closed, continuously flowing system. No aeration was needed, but filtration was necessary. Filtration was needed for two reasons: to prevent snails from moving from one culture to the other by the water flow, and to remove undesirable materials or small living organisms, e.g., debris, fungi, insect larvae, etc.

b. Water storage tanks. Cylindrical plastic tanks were used as water reservoirs. The water storage tank was connected to a water pump by a PVC pipe (3/4 inch in diameter) and connected to the culturing container by a wooden drain.

c. Water pumps. A submersible, magnet-driven water pump (type 2-SMD, Little Giant Pump Co., Oklahoma City, Oklahoma, U.S.A., efficiency of driven water about 375 gal/hr at 10 ft) was used to circulate the water. The flow rate in the artificial stream could be adjusted by using valves or a water bypass. The pump could service five to six artificial streams of the size used in this study.

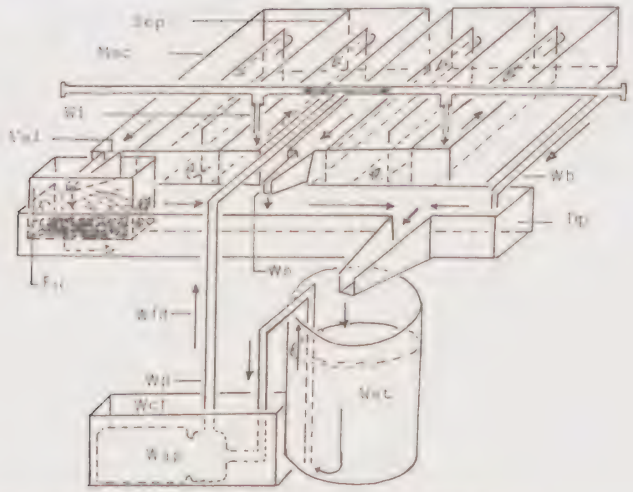

FIG. 19. Diagram of the modified type of artificial stream aquaria.
Abbreviations: Dp = drain passage; Fic = filter container; Msc = main stream container; Sep = septum; Val = valve; Wap = water pump; Wb = water bypass; Wct = water cooling container; Wfd = water flow direction; Wi = water inlet; Wo = water outlet; Wp = water pipe; Wst = water storage container.

d. Water pipes (PVC pipes). Two sizes of pipes, 1/2 inch and 3/4 inch in diameter, were used for connecting the water pump to the culturing containers and to the water reservoirs as described previously.

e. Drain. The drain passage was made of wood. Its size was about 300 cm long, 20 cm wide and 15 cm deep.

All types of containers were prepared in the same manner by putting mud mounds on the bottom and adding small rocks. The amounts of rocks and mud used were adjusted according to the size of the containers. Conditioned water and diatoms were added at least 5-7 days prior to starting the experiment. The water was aerated in the glass tanks and in some of the crystallizing dish viviaria. All culture or maintenance aquaria were covered by glass plates. The water was changed when necessary.

Results and discussion

The objectives of this section of the study were: (1) to maintain field-collected *Tricula aperta* snails while they grew to maturity for cytotaxonomic and enzymatic activity studies or to keep them alive through a particular schistosome susceptibility test; and (2) to develop a dependable culture method for these snails for future studies. Since the numbers of snails obtained from the field were not enough for all the studies planned, most snails used in the culture and maintenance studies were later transferred to other research. Therefore, no numerical data were recorded for the maintenance of *T. aperta* except for the comparative results of culturing the alpha race in the prototype of the artificial stream and the Petri dish vivaria. However, all subjective results of the study were recorded and are reported below.

Both species of diatoms, *Navicula pelliculosa* and *Achnanthes exigua* var. *agterovalva*, were excellent for feeding *Tricula aperta* snails during this study. Van der Schalie & Davis (1965) reported that young oncomelanid snails grew better on soil containing green algae and diatoms than other food. Diatoms have been reported elsewhere as being a good source of energy for snails. In field studies, van Someren (1946) found that a habitat of *Lymnaea* (=*Radix*) *caillaudi* was characterized by a certain amount of macrophytic vegetation and a

rich assortment of diatoms, desmids and other microscopic algae, which usually covered the aquatic plants. Kitikoon & Schneider (1976) reported that a good habitat for the gamma race of *T. aperta* was in areas dominated by water shrubs (*Homonoia* spp.), and which contained rocks, dead leaves and twigs with plenty of diatoms (*Navicula* spp.). The gamma snails were not found in areas dominated by long strands of filamentous green algae. Lohachit et al. (1980) reported that diatoms were good food for *T. aperta* snails.

The method of culturing diatoms which I developed proved excellent in all aspects, i.e., mass production could be increased very rapidly, the culture could be recycled, and the method was easy, dependable and cheap.

The blue-green algae, *Nostoc muscorum*, also was very good food for culturing *Tricula aperta*, especially when algae from a new culture was used. It was the first choice if substitution for diatoms was necessary. Liang (1974) was successful in culturing *Bulinus globosus* and *Biomphalaria pfeifferi* by using *N. muscorum* on a mud substrate. Liang & van der Schalie (1975) reported that *N. muscorum* was a good source of food for the gamma race of *T. aperta*.

Multivitamins, vitamin B complex and vitamin E were not used for culturing *Tricula aperta* snails, because my tests showed that multivitamins and B complex vitamins clouded the water and promoted an overgrowth of bacteria and fungi in the culture, and vitamin E did not dissolve in the water. The latter also caused an overgrowth of bacteria and fungi in the culture.

Calcium carbonate did not give any side effects to the cultures during my studies, since it was used in only small quantities (about 10 mg mixed with 500 g of dry soil). However, calcium seemed to promote shell growth. Calcium is important in shell formation, but its concentration in water favorable to snails seemed to vary greatly. Malek (1958) observed that snails can live in calcium-poor water. Frank (1963) found that *Biomphalaria pfeifferi* grew faster and deposited more eggs in water low in calcium (13 ppm as $CaCO_3$) and had higher mortality rates in higher calcium concentrations (up to 31 ppm $CaCO_3$) in the laboratory. On the other hand, *Bi. glabrata* and *Bulinus truncatus* could tolerate calcium ions (as $CaCO_3$) up to saturated concentration (Deschiens, 1954). Normally, *Bulinus* and *Biomphalaria* habitats were found to be rich in calcium (Alves, 1958). Harry et al. (1957) found that the optimum concentration of calcium for *Bi. glabrata* in nature ranged from 17-70 ppm. Results of my studies showed that calcium concentration in the habitat of the gamma race of *Tricula aperta* at Khong Island was 70-80 ppm (Kitikoon & Schneider, 1976). The calcium concentration in aquaria was not measured during this study.

Although snails appeared to like ground maple leaves, many died by the following day after consuming a large amount (as indicated by faecal pellets). The cause of death was not known. The maple leaves may have contained toxic substances, or the snails may have died because of suffocation due to fermentation of the leaves.

Filter paper may be the second choice in substituting for diatoms when the supply of the latter is short. The *Tricula* snails usually started to eat the filter paper two or three days after it was introduced into the cultures. The value of filter paper has been noted before. McMullen (1949) used filter paper as a food additive for maintaining *Oncomelania* snails. Wagner (1954-1955) showed that oncomelanid snails could live longer on filter paper than on other substrates.

Obviously, the mud substrate played an important role in the *Tricula aperta* cultures. I found that the cultures which contained a mud substrate improved considerably in various aspects, i.e., the snails were healthier and grew faster, especially in the young. These observations agreed with those of many authors, e.g., Gordon et al. (1934), Cowper (1946), Ward et al. (1947), Standen (1949), Pan (1958), Watson (1958), van der Schalie & Davis (1965) and Chu et al. (1966a,b). I found that newly hatched snails preferred to live in the soil substratum until they were about one-third grown. This also was true in the natural habitat. All very young snails of *T. aperta*, especially those of the gamma race, clung underneath or at the

sides of the rocks near their junctions with the soil substrate. Therefore, the soil substrate may provide some essential substances for snail growth.

Selection of soil for culturing *Tricula aperta* was critical. Soil too rich in organic matter was found to be worthless because fermentation processes continued in the cultures, causing the snails to die. (However, other snails, i.e., *Bulinus truncatus*, have been reported to prefer mud rich in organic matter (Watson, 1958).) Clay soil was too sticky and clouded the water. The most preferable soil was a mixture of organic matter, clay and silty soil. The best ratio of these three components to use, however, was not studied.

Chemical analysis of the water was not done. However, the quality of water used during my studies seemed to undergo seasonal fluctuation, especially in regard to dissolved chlorine, which had severe effects on the snail cultures. Part of this problem was corrected by boiling the water, adding a 5% solution of sodium thiosulphate (1 ml/10 gal water) and aerating the water for 48 hrs prior to use.

Water quality might be one of the most important factors in maintaining and culturing snails. Most investigators seek biologically conditioned water for culturing snails. Various types of water from different sources have been selected for use in snail cultures. Methods of conditioning water have been established. Cowper (1946) used mud for conditioning the rain or tap water used for culturing *Bulinus truncatus*. Chernin & Michelson (1957) reported that watercress-conditioned tap water was necessary for *Biomphalaria glabrata*. Claugher (1960) stated that tap water conditioned by maintaining guppies in it for two weeks was desirable for *Bulinus* snails. Chu et al. (1966a,b) found that stored rain water was most suitable for *Bu. truncatus*. The water flea, *Daphnia*, and coontail water weed, *Ceratophyllum*, were used to condition water for maintaining *Bu. africanus* by Kinoti (1968).

Other workers have used non-biologically conditioned water for their cultures. Chernin (1957) used aerated distilled water to study the effect of water volume on the growth of *Biomphalaria glabrata*. Tap water dechlorinated by sand and activated charcoal was successfully used by Lee & Lewert (1956) in raising *B. glabrata* and *B. pfeifferi*. Spring water was employed in the experiments of Pelligrino & Goncalves (1965) and Sturrock & Sturrock (1970).

In addition to biologically and physically conditioned water, water chemistry has been of interest to many authors. Studies on water chemistry have emphasized mostly minerals (in terms of inorganic compounds), ions and pH values. Colton (1908) concluded that saturated solutions of calcium salts ($CaSO_4$) seemed to benefit the growth of *Lymnaea*. Boycott (1936) stated that the most populous snail habitats in Britain were actually calcium-rich rivers, lakes and canals. On the other hand, Harry & Cumbie (1956a,b) stated that in Puerto Rico streams coming from limestone or sources of lime formation are not favorable places for aquatic snails. Harry & Aldrich (1958) found in the laboratory that zinc, copper, cadmium and silver, with a range of concentrations between 0.050 to 0.100 ppm in distilled water, will adversely stress *Biomphalaria glabrata*, and higher concentrations will kill the snails very rapidly.

Some data on water chemistry at the habitat of the gamma race of *Tricula aperta* in the Mekong River at Ban Xieng Wang, Khong Island, Sithandone Province, Laos, were given by Kitikoon & Schneider (1976). These follow. Total dissolved solid, 140-170 ppm; conductivity (= Ec x 10^{-6} @ 25°C), 240-250 ppm; pH, 7.8-8.4 (diurnal only); dissolved oxygen, 6.2-7.5 ppm (the percentage of saturation was from 78-103% (the last value indicating supersaturation)); alkalinity, 70-80 ppm $CaCO_3$; total hardness, 70-75 ppm $CaCO_3$; and carbon dioxide, 4-10 ppm.

These data undoubtedly indicate favorable water chemistry for culturing and maintaining *Tricula aperta* in the laboratory. The pH values during my study were 7.8-8.2.

Light and temperature used during the study seemed not to cause any side effects, since these two factors could be adjusted physically. Although there have been many studies on

the effect of temperature on snail behavior, little attention has been given to the effect of light. According to the geographical location (at the 14th parallel in Southeast Asia) of the alpha, beta and gamma races of *Tricula aperta*, the length of days and nights are almost equal all year round. Therefore, light may be among the factors which influence snail habits. I found that the *T. aperta* snails lived both in the shade and in open sunlight. The gamma race preferred to crawl on top of the rocks (except when they were very young), while the alpha race tended to live underneath the rocks, and the beta race exhibited both of these tendencies.

Van der Schalie & Davis (1965) indicated that the growth rate of the hydrobiid snail *Oncomelania hupensis formosana* was highest when it was kept under continuous white-cool-fluorescent light (40 watts) suspended 10 inches above the cultures. Similar results were found by Joy (1971) for *Biomphalaria glabrata*, where the highest rate of egg-laying occurred when the snails were maintained under continuous light with an intensity of 355 Uw/cm^2. Determination of light optima for culturing *Tricula aperta* may be extremely useful. I followed van der Schalie & Davis (1965), but used 12-hr light and dark intervals for my snail cultures.

Air and water temperature at the *Tricula aperta* habitats varied from place to place and from time to time. From my observations in March to June, 1974, the water temperatures ranged from 24-33°C and varied according to the depth of water. The air temperatures ranged from 25-35°C at the principal collecting sites in the Mekong and Mune rivers (Kitikoon & Schneider, 1976).

The optimum temperature for culturing *Tricula aperta* snails has never been determined. However, the room temperature for culturing these snails, as used by various authors, ranged from 25-29°C, e.g., 25-27°C for Liang & Kitikoon (1980), 25-29°C for Lohachit et al. (1980), and I used 22-28°C. Liang & van der Schalie (1975) did not report the temperatures they used.

Most information on culture temperatures was from studies on *Oncomelania* subspecies (Gastropoda: Hydrobiidae) and pulmonate snails, and is summarized below.

The reported optimum temperatures used for culturing oncomelanid snails showed some variations. DeWitt (1952) reported that four subspecies of *Oncomelania hupensis* reproduced throughout the year at temperatures ranging from 26-28°C. Wagner & Wong (1956) and Chi & Wagner (1957) observed that the greatest reproduction of young for *O. h. nosophora, O. h. quadrasi* and *O. h. formosana* occurred at 26°C. They also mentioned that at this temperature the snails had a moderate rate of mortality. Subsequently, van der Schalie & Getz (1963) studied the response of *Oncomelania* to soil and temperature gradients and reported that the average temperature preference was 21°C for *O. h. hupensis*, 23°C for *O. h. formosana*, 25°C for *O. h. nosophora* and 26°C for *O. h. quadrasi*. Van der Schalie & Davis (1965) observed that the greatest growth rate in four subspecies of *O. hupensis* was at 25 ± 2°C. Davis (1972) stated that the room temperature for *Oncomelania* mass culture should be maintained at 25-26°C at all times.

In regard to pulmonate snail cultures, Gordon et al. (1934) found that the lowest death rate of *Biomphalaria pfeifferi* was at 25-30°C. They also stated that the maximum oviposition in *Bulinus globosus* occurred from 25-26°C. Subsequently, many workers cultured their snails at 20-30°C. Recently, van der Schalie & Berry (1973) found that none of six pulmonate species (*Lymnaea stagnalis, L. emarginata, Helisoma trivolvis, H. anceps, H. campanulatum* and *Physa gyrina*) and one gill-breathing operculate (*Amnicola limosa*) did not reproduce when the temperature exceeded 30°C in the laboratory. However, they stated that growth was usually better in "warm" water, but the advantages in growth were generally offset by a lack of gonad development. The optimum temperatures given by the World Health Organization (1957) for the general culture of snail intermediate hosts of schistosomiasis was between 22-26°C.

I have measured water temperatures at noon in a pool where the alpha race of *Tricula*

aperta occurred. These were 28°C in the shade and 35°C in direct sunlight (at the bottom of the pool). The snails were abundant, but they tended to crawl beneath rocks or to the cooler areas.

Temperature may influence egg hatching, but as yet no data on this subject have been reported. However, I observed that the eggs hatched faster at 28-30°C than at 22-24°C (unpubl. data). From this point of view, temperature seemed to be a major physical influence in the culturing of snails. The optimum temperature for culturing *Tricula aperta* is not yet known, but it may be between 25° and 30°C. Pinpointing the optimum temperature will be a great contribution to the culturing and maintenance of *T. aperta*.

In general, containers play an important role in culturing and maintaining snails in the laboratory. However, one might assume that the best types of containers to use for various snails might vary and not all kinds of containers could be used successfully for both culture and maintenance. The results of my own studies showed this, i.e., the kinds of containers which were best for culturing and for maintaining *Tricula aperta* were different. However, not all kinds of containers listed previously were used for both culturing and maintaining these snails during the study. Most of my studies dealt with maintenance, except for a prototype of an artificial stream and Petri dish aquaria which were used solely for comparison of culturing containers. The results of these studies are reported below.

The results of culture of the alpha race of *Tricula aperta* in terms of mortality rates and egg production and hatchability, obtained from an artificial stream and Petri dish vivaria, were clearly different. Numbers of dead snails and the mortality rates observed during four corresponding months in both types of cultures are shown in Table 2. The overall mortality rates of the alpha race of *T. aperta* in the artificial stream and Petri dish aquaria were 39% and 65%, respectively. The number of eggs laid and the numbers of newly hatched young found during six consecutive months are shown in Table 3. The total number of eggs and hatched young in the artificial stream aquarium were 154 and 123 (80%), respectively, whereas the total eggs and total hatched young obtained from the Petri dish vivaria were 28 and 7 (25%), respectively.

The mortality rates of the alpha race of *Tricula aperta* in the artificial stream and Petri dish vivaria were statistically significantly different ($P < 0.0005$; Chi-square test, see Table 2).

TABLE 2. Comparison of the mortality of the alpha race of *Tricula aperta* in a prototype of artificial stream and Petri dish vivaria during four consecutive months.[1]

Month No.	Artificial stream aquarium			Petri dish vivaria		
	No. snails	No. dead	Mortality %	No. snails	No. dead	Mortality %
1	150*	8	5	100*	11	11
2	142	17	12	89	15	17
3	125	18	14	74	26	36
4	107	15	14	48	13	27
Total	150	58	39	100	65	65

[1] Chi-square test for independence was used to test for differences of the mortality rates ($P < 0.0005$).

* = Initial number of snails used in the first month.

TABLE 3. Comparison of the number of eggs laid and the number of newly hatched snails in a prototype of an artificial stream and Petri dish vivaria in six consecutive months.[1]

Month No.	Artificial stream aquarium		Petri dish vivaria	
	No. eggs observed	No. newly hatched snails	No. eggs observed	No. newly hatched snails
1	12	0	10	0
2	22	4	10	0
3	40	17	4	4
4	80	30	4	2
5	*	45	*	1
6	*	27	*	0
Total	154	123 (80%)	28	7 (25%)

[1]Chi-square test for independence was used to test for the differences in the hatchability rates ($P<0.0005$).

* = Snails were taken out of both artificial stream and Petri dish vivaria at the end of the fourth week.

The death rate was much lower in the artificial stream than in the Petri dish vivaria. The numbers of eggs laid in the two types of vivaria could be compared only roughly, since the exact number of eggs present in the artificial stream aquarium was not known. The number of eggs found in the artificial stream aquarium was undoubtedly underestimated, whereas the number counted in the Petri dish culture was accurate, since the exact number of eggs could be observed easily by viewing the whole culture under a stereomicroscope. Nevertheless, the snails laid more eggs in the artificial stream aquarium than in the Petri dish vivaria. Hatchability of eggs in the artificial stream aquarium (80%) was much higher than in the Petri dish vivaria (25%) ($P<0.0005$; Chi-square test, see Table 3). Due to the constant flow in the stream, the water was probably saturated with oxygen and influenced the fully developed eggs to hatch. A peculiar phenomenon could be observed in the artificial stream aquarium in that the number of eggs laid gradually increased and this coincided with increasing death rates. The reverse results occurred in the Petri dish vivaria. Therefore, results from this study indicated that the artificial stream aquarium was better than the Petri dish vivaria both for culturing and maintaining *T. aperta* in the laboratory. However, there were some disadvantages in the artificial stream aquarium, i.e., it was easily contaminated with fungi, insect larvae and ostracods. These problems will be discussed later.

The maintenance of *Tricula aperta* in Petri dish vivaria was not successful. Most of the snails died, especially the newly introduced field-collected snails. The cause of this was not known. The snails died faster when the numbers used exceeded 50 snails/Petri dish. Those that lived (more than half of those initially used) did not grow well. This may have been due to overcrowding. To keep the snails alive when using 15-20 snails per culture, the culture had to be changed periodically in order to maintain optimum conditions. Therefore, too much effort and time were consumed in maintaining just a small number of snails in this type of vivarium. For that reason it was considered a failure.

Crystallizing dishes and small bottle containers were equally excellent for maintaining all

three races of *Tricula aperta* during my study. The snails were healthier, grew faster and had lower mortalities than those which were maintained in Petri dishes and glass "tanks" or aquaria. The crystallizing dishes and small bottles could be operated with or without water aeration.

The *Tricula aperta* snails were rather inactive when kept in containers, which, in containers that were too large, caused a problem in feeding, i.e., in reaching their food. However, this seemed to be corrected by using crystallizing dishes and small bottle containers. These two types of aquaria were not too large for *T. aperta* snails when searching for food.

Glass tanks were not good for maintaining *Tricula aperta*, but were found to be excellent for use in acclimatizing field-collected snails prior to culturing or maintenance. The snails did not grow well and became stunted if they were kept for too long a time in this type of container. The causes of slow growth and stunting in snails have been explained previously by other authors, and will be discussed later in this paper. However, the major cause here might be due to less food consumption, because the snails preferred to cling onto the sides of the containers near the water surface, while the food supply and essential substrates (diatoms and mud) were deposited in the bottom of the large container. Therefore, the snails had less chance to feed.

Modified types of artificial stream aquaria were not used to complete the study, since the cultures were contaminated with fungi. Therefore, the study was terminated in order to save those snails for other research. However, I found many eggs were deposited on the rocks and the sides of the containers. These culturing experiments should be continued, but the contamination problems would have to be resolved prior to restarting. I am confident that the modified artificial stream aquaria will prove to be one of the best for culturing and maintaining *Tricula aperta* snails, but other methods of culturing and rearing still need to be established and tested.

Previous investigators have designed their cultures to resemble the natural habitat as nearly as possible. To produce the amphibious natural environment of *Oncomelania*, the cultures were prepared with attention to slope of soil, type of soil, and whether or not and how to aerate the water, etc. Vogel (1948) referred to such cultures as aquaterraria. Various aquaterraria have been used in *Oncomelania* cultures. Bauman et al. (1948) prepared a mud bank with a water reservoir, while Moose & Williams (1965; quoted by van der Schalie & Davis, 1968) preferred to use jars for holding large numbers of snails (200 per jar) for six to seven months. They covered the jar bottoms with moist filter paper. Van der Schalie & Davis (1965) emphasized that the Petri dish cultures were the best for rearing young snails to maturity, but were not suitable as vivaria for maintaining adults or encouraging production of young. Van der Schalie & Davis (1968) found that the medium clay pot was superior for both adult survival and the production of young. French (1974) concluded that the surface area and the arrangement of the mud were significant factors in both breeding and rearing oncomelanid snails in the laboratory.

Most types of aquaria or tanks have been used successfully in culturing aquatic non-amphibious pulmonate snails. These have been enamel trays for *Bulinus nasutus* (McClelland, 1964), battery jars for *Biomphalaria glabrata* (Chernin, 1957; Ritchie et al., 1966; Jobin & Michelson, 1967), plastic tanks for *Bi. pfeifferi* (Sodeman, 1970) and glass tanks for *Bulinus* snails (Claugher, 1960). Liang (1974) reported more details of his success in culturing *Bi. pfeifferi* and *Bulinus* snails by using plastic and glass tanks, respectively.

Population density has long been observed by various authors as one of the important factors in culturing snails. Turner (1927) found a marked stunting in two species of *Lymnaea* due to overcrowding. Wright (1956) suggested that overcrowding might cause dwarfing of snails because of an accumulation of excretory products in the water. Later, Wright (1960) discussed the possibility of three factors causing stunting: food, collision and chemical pollution (pheromones). He believed that even low concentrations of pheromones could inhibit

growth and fecundity. Berrie & Visser (1963) extracted a substance, mono-hydroxy-tricarboxylic acid-mono-isodecyl-dimethyl ester ($Cl_8H_{32}O_7$), from water inhabited by *Biomphalaria sudanica* which inhibited the growth of these snails in the laboratory. Presumably, this substance was a metabolite of the snails.

The number of snails used in a culture normally varied according to the size of the aquarium. In culturing and rearing oncomelanid snails, Abbott (1948) recommended using no more than 100 snails per aquarium of 12 inches in diameter. Moose & Williams (1961-1962) used 50 snails in each of their plastic tray cultures. Wagner & Wong (1956) and Chi & Wagner (1957) recommended using eight to nine adults per Petri dish vivarium. Van der Schalie and Davis (1965) found that the optimum growth rate for *Oncomelania* snails occurred when one or two newly hatched snails were used in a 9 cm diameter Petri dish culture. They also reported that increasing the number of snails per culture to 5-10 caused stunting and decrease in growth rate and development. Liang & van der Schalie (1975) used 10 half-grown *Tricula aperta*, gamma race, per Petri dish culture.

Therefore, the importance of population density in culturing snails is obvious. By using the optimum number of snails per culture, higher reproduction and growth rates will be realized.

Parasites and predators are obviously major problems in culturing and maintaining snails in the laboratory. These include bacteria, protozoa, algae, fungi, flatworms, nematodes, annelids, rotifers and arthropod larvae (i.e., *Polypedlum anale*, which invaded and destroyed egg-masses of *Bulinus globosus*). Lo (1967) reported that two species of ostracods, *Cypridopsis vidua* and *Cypricercus reticulatus*, caused *Biomphalaria glabrata* to withdraw into their shells. He also stated that the snail egg-masses were destroyed when the population levels of ostracods became high, or when the other food of ostracods was not sufficient.

I found that ostracods (*Cypridopsis vidua* and *Cypricercus reticulatus*) and insect larvae (family Bibionidae) caused major disturbances to the snail cultures. The insect larvae destroyed the eggs and the snails. The larvae usually made their cases on the snail's shell, stuck out their heads and moved their anterior bodies back and forth in the vicinity of the snail's aperture. The snails were very sensitive to such moving objects and withdrew their heads into their shells and closed the shell apertures very tightly with their opercula. This may have caused some of the snails to die due to suffocation or starvation. Finally, these larvae moved into the dead snails' shells and ate the flesh. Ostracods did almost the same thing by disturbing the snails' feeding. After the death of the snails, the ostracods ate the flesh.

Ostracods are difficult to control in snail cultures since they are parthenogenetic and generations are produced very rapidly. The best way to control ostracods is by terminating the contaminated containers and then cleaning them as follows: the contaminated containers were washed in running tap water (70-80°C) for several minutes, or soaked in 5-10% formalin overnight and then thoroughly rinsed. To control the insect larvae, the procedure above may be followed, but the use of formalin is not necessary.

Biological control using guppy fish as an alternative procedure may be used for controlling both insect larvae and ostracods, if the contaminated cultures need to be continued. However, the effects of the guppies on the cultures should be tested prior to use. Finally, other control methods for parasites and predators of the snails in the cultures should be established in order to get higher yields of snails for research.

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STUDIES ON *TRICULA APERTA* AND RELATED TAXA, THE SNAIL INTERMEDIATE HOSTS OF *SCHISTOSOMA MEKONGI*. III. SUSCEPTIBILITY STUDIES

Viroj Kitikoon

ABSTRACT

Susceptibility of snails from five morphological populations of *Tricula aperta* and from one population of *"Manningiella" conica* to infection with *Schistosoma mekongi* was studied. All of the populations tested were found to be susceptible to *S. mekongi*, but to different degrees. The beta race of *T. aperta* showed the highest susceptibility rate (60%).

INTRODUCTION

Susceptibility tests for the molluscan intermediate host(s) of the Mekong schistosome have been a subject of interest to many researchers ever since Barbier (1966) reported the occurrence of human schistosomiasis at Khong Island, Laos. Harinasuta et al. (1972) were the first to demonstrate the life cycle of *Schistosoma mekongi* Voge, Bruckner and Bruce (previously called *S. "japonicum"* or *"S. japonicum*-like trematode") in the laboratory using a field-collected gamma race of *Lithoglyphopsis* (= *Tricula*) *aperta* Temcharoen. They reported the susceptibility rate of these snails to be 29%. Sornmani et al. (1973) reported more details of that study. Later, Kitikoon et al. (1973) found that the natural infection of the Mekong schistosome in the gamma race of *Tricula aperta* at the endemic focus was 0.03%. In 1974, I found that two more races of *T. aperta* (including two sibling races of the gamma snails) and *Manningiella conica* Temcharoen were capable of carrying the Mekong schistosome in the laboratory (unpubl. data, now being reported in this paper). Sornmani (1976) reviewed the current status of the Mekong schistosome, which included the infection rates of the parasite in the alpha, beta and gamma races of *T. aperta*. Without giving further details of the study, the susceptibilities reported were 2.7%, 51.5% and 10.5%, respectively. Liang & Kitikoon (1980) reported that the susceptibilities of pure laboratory strains of alpha and beta races of *T. aperta* to *S. mekongi* were 12% and 60%, respectively.

The main purposes of the above studies were obviously initially limited to looking for a molluscan intermediate host(s), in order to complete the life cycle of the Mekong schistosome and to identify this newly found human parasite. The objectives of the susceptibility studies which I conducted in 1974 and which are reported in this paper for the first time were more or less the same as those mentioned above (i.e., in terms of searching for the snail intermediate hosts of the Mekong *Schistosoma*). But, in addition, I wanted to obtain comparative susceptibility data on the alpha, beta and gamma races of *Tricula aperta*, since these three races of snails are phenotypically different.

MATERIALS AND METHODS

Snails

Two species of snails, *Tricula aperta* and *Manningiella conica* (see figs. 2-8 in Kitikoon et al., 1981), were tested for susceptibility to *Schistosoma mekongi*. The *T. aperta* snails tested included the alpha, beta and gamma races, plus two additional phenotypes of the gamma race. (The latter two phenotypes may represent two additional sibling races or possibly new species.) Specimens used for testing were all field-collected from the different localities. The alpha, beta, gamma, non-pigmented and pigmented populations

of *T. aperta* and the *M. conica* snails were from Ban Khi Lek, Kaeng Kao, Ban Na, Sompamit Falls and Moung Khong Hospital (see figs. 9E, 11C, 12, Kitikoon et al., 1981), respectively.

Snails were maintained in the laboratory for 60 days prior to testing. During maintenance, the snails were checked periodically for natural trematode infections by searching for shedding cercariae. Positive snails, when they occurred, were removed. Prior to experimentation, each group of snails was divided into three lots. One lot was crushed and examined microscopically for the presence of rediae, sporocysts, cercariae and metacercariae of other trematodes. The second lot, which was presumably negative, was used for susceptibility testing, and the third lot was used as an experimental control.

Miracidia

Miracidia used in these experiments were derived from eggs from naturally infected dogs on Khong Island, Laos. The hatching technique followed Pesigan & Yogore (1947). Only freshly hatched and active miracidia were used.

Exposures

Exposure of the snails to miracidia of *Schistosoma mekongi* was done in micro-dishes. Snails were exposed individually to five miracidia for 2 hrs. Control and exposed snails were then kept in aerated glass aquaria at room temperature (25-28°C) and fed diatoms regularly. After the fourth week, both exposed and control snails were examined at 3-day intervals for presence of cercariae of the Mekong schistosome by en masse shedding in a square watch glass under an electric lamp. Shedding was stopped after 1 hr in order to prevent death of the snails from exhaustion. At the sixth week, shedding was performed daily for 1 hr. In those lots in which there were positive snails, individual shedding was done at 3 or 4-day intervals by placing the snails individually into micro-dishes following the above procedure. A stereomicroscope was used for viewing the fork-tailed cercariae of *S. mekongi* directly in the shedding container. After 60 days post-exposure, snails which had not shed cercariae were crushed and examined microscopically for the presence of sporocysts or cercaria of *S. mekongi*.

RESULTS

None of the field-collected snails used during the susceptibility tests were found to be naturally infected with *Schistosoma mekongi*. Some, however, were found to be infected with unknown species of trematodes (Table 1). No attempt to identify these other parasites was made. Trematode infections other than *S. mekongi* in control and exposed lots were not recorded. The snails in the control lots were all negative (Table 2).

Results of susceptibility tests (including infection rates, prepatent periods, etc.) to *Schistosoma mekongi* of the three races of *Tricula aperta* (plus the two other sibling races or species) and *Manningiella conica* are shown in Table 2. The overall infection rates were 4%, 60%, 13%, 4%, 47% and 12% in the alpha, beta, gamma, non-pigmented, pigmented and *M. conica* snails, respectively. The sporocysts found in the gamma race of *T. aperta* and in *M. conica* contained only very immature cercariae.

The positive groups of these snails (Table 2) were then tested to see if there were significant differences in susceptibility using the Chi-square test (two-way contingency table procedure) at the 1% level of significance. The overall result showed that the alpha, beta, gamma, non-pigmented, pigmented and *Manningiella conica* snails had significant differences ($P<0.0005$) in regard to susceptibilities. But, when pairwise comparisons were done by using the same procedure and level of significance as mentioned above, the results (Table 3) showed that the susceptibility rate of the alpha race to infection with *Schistosoma mekongi* was very significantly different from those of the beta ($P<0.0005$) and gamma ($P<0.005$) races, and *M. conica* ($P<0.005$), but not different from the non-pigmented ($0.90<P<0.95$) snails. The susceptibility rates of the alpha (4%) and non-pigmented (4%) snails were comparatively low as compared to the beta (60%) snails. The susceptibility rate of the beta race was definitely significantly different from those of alpha ($P<0.0005$), gamma ($P<0.0005$) and non-pigmented ($P<0.0005$) snails, and *M. conica* ($P<0.0005$), but not different from pigmented ($0.30<P<0.40$) snails. The susceptibility rates of the beta (60%) and pigmented (47%) snails were very high as compared to the alpha snails. The susceptibility rate of the gamma

TABLE 1. Results of tests for natural trematode infections in field-collected *Tricula aperta* and *Manningiella conica* snails prior to their use in susceptibility experiments.

Races or species	Shedding			Crushing[1]				
	No. of individuals tested	No. pos. cercariae		No. of individuals tested	No. pos. cercariae		No. pos. spt.	No. pos. met.[2]
		Single	Fork		Single	Fork		
T. aperta								
alpha	450	0	0	100	0	0	0	12 (12%)
beta	400	0	0	100	0	0	0	8 (8%)
gamma	400	0	0	100	0	0	0	2 (2%)
non-pigmented	360	0	0	50	0	0	0	4 (8%)
pigmented	30	0	0	10	0	0	0	1 (10%)
M. conica	390	0	0	50	0	0	0	3 (6%)

[1] The snails used for crushing were from the left column (after cercarial shedding).

[2] Species not identified.

Abbreviations: fork = fork-tailed cercariae; met. = metacercariae; pos. = positive; single = single-tailed cercariae; spt. = sporocysts.

race was statistically different from the alpha and beta races mentioned above and the non-pigmented ($P<0.005$) snails, but not from *M. conica* ($0.60<P<0.70$). The susceptibility rates of the gamma race (13%) and of *M. conica* (12%) were medium as compared to those of the alpha (4%) and beta (60%) snails. The susceptibility rate of the non-pigmented race also was significantly different from *M. conica* ($P<0.005$) and the beta and gamma races, but not from alpha snails as mentioned above. The pairwise comparisons of pigmented, alpha, gamma, non-pigmented and *M. conica* snails were not calculated, since the expected frequency of the infected snails was not sufficient to yield a good Chi-square approximation.

DISCUSSION

The results from my studies on susceptibility were striking in that the snails capable of being infected with *Schistosoma mekongi* were riverine species rather than amphibious snails of rice paddies and similar habitats. So far, six kinds of snails (two of which are possibly sibling races or species of the gamma snails, and one a snail of a nominally different genus,

TABLE 2. Results of susceptibility tests[1] of *Tricula aperta* and *Manningiella conica* to infection with *Schistosoma mekongi*.

Races or species	Experiments				Controls		
	No. exposed	P.P. (days)	No. positive	No. survived	No. used	No. positive	No. survived
T. aperta							
alpha	250	53-54	8 (4%)[2]	209	100	0	65
beta	200	42-43	103 (60%)	172	100	0	85
gamma	200	44-48	21(1)[3] (13%)	158	100	0	75
non-pigmented	200	45-59	7 (4%)	186	100	0	80
pigmented	15	46	7 (47%)	15	ND	ND	ND
M. conica	200	44	22(7)[3] (12%)	190	100	0	85

[1]Test for overall susceptibility differences using two-way contingency table at 1% level of significance, $P<0.0005$.

[2]% susceptibility rate = $\frac{\text{No. positive}}{\text{No. survived}} \times 100$

[3]Number of snails found positive for sporocysts by crushing.

Abbreviations: ND = not done; P.P. = prepatent period.

Manningiella conica) were found capable of carrying *S. mekongi* in the laboratory. Therefore, this newly found human parasitic trematode would seem not to be highly selective in its snail intermediate hosts. But, since other trematode parasites are usually quite host specific (or if several host species are involved, the hosts are closely related to each other), all of these snails susceptible to *S. mekongi* may belong to the same closely related group, even though belonging to different races or species.

Davis (1979) suggested that *Manningiella conica* is closely related to *Tricula*. He synonymized *Manningiella* with *Hubendickia* and transferred all species formerly put in *Manningiella*, except *M. conica*, to other genera. On parasitological evidence, I assume that *M. conica* should be transferred to the genus *Tricula*. This would seem reasonable since these snails were comparatively quite susceptible to *S. mekongi*. Also, another two phenotypes (unnamed taxa) or so-called sibling races of the gamma snails, i.e., the non-pigmented and pigmented populations used in the present study, undoubtedly belong to the genus *Tricula* as far as shell morphology and susceptibility to the Mekong schistosome are concerned. A final conclusion in regard to the two unnamed taxa, however, cannot be made until further studies

TABLE 3. Results of pairwise comparisons of the susceptibility rates between the alpha, beta, gamma, non-pigmented, pigmented and *Manningiella conica* snails to infection with *Schistosoma mekongi*, using the Chi-square test at 1% level of significance.

Pairs	Probability	Significance
Alpha: beta	$P<0.0005$	S
Alpha: gamma	$P<0.005$	S
Alpha: non-pigmented	$0.90<P<0.95$	NS
Alpha: pigmented	ND	ND
Alpha: *M. conica*	$P<0.005$	S
Beta: gamma	$P<0.0005$	S
Beta: non-pigmented	$P<0.0005$	S
Beta: pigmented	$0.30<P<0.40$	NS
Beta: *M. conica*	$P<0.0005$	S
Gamma: non-pigmented	$P<0.005$	S
Gamma: pigmented	ND	ND
Gamma: *M. conica*	$0.60<P<0.70$	NS
Non-pigmented: pigmented	ND	ND
Non-pigmented: *M. conica*	$P<0.005$	S
Pigmented: *M. conica*	ND	ND

Abbreviations: ND = not done due to insufficient expected frequency; NS = no significant differences; S = significant differences.

(anatomy, cytology, isozymes, etc.) of these snails are undertaken.

Susceptibility rates of the alpha, beta and gamma races of *Tricula aperta* to *Schistosoma mekongi* reported by various workers (Harinasuta et al., 1972; Sornmani et al., 1973; Sornmani, 1976; Liang & Kitikoon, 1980; Kitikoon, present study (Tables 2 and 3)) were very different. (Harinasuta et al. (1972) reported only the susceptibility rate of the gamma race of *T. aperta*; Liang & Kitikoon (1980) excluded this race.) The results for the gamma snails as obtained by Harinasuta et al. (1972) seemed very high in comparison to the other authors. The susceptibility results for all three races of *T. aperta* obtained by Sornmani (1976) were lower than those reported by Liang & Kitikoon (1980) and Kitikoon (present study). My current results agree with those of Liang & Kitikoon (1980).

The differences in susceptibility rates might be caused by the method of calculating susceptibilities, by the ages of the snails, or by the sources of the snails used. The method used here for calculating the susceptibility or infection rate is as follows.

$$\text{Susceptibility rate} = \frac{\text{No. of positive or infected snails}}{\text{No. of snails which survived}} \times 100.$$

Liang & Kitikoon (1980) followed this method, but Sornmani (1976) may have followed the method where:

$$\text{Susceptibility rate} = \frac{\text{No. of positive or infected snails}}{\text{No. of snails used}} \times 100.$$

These two methods will yield the same results if all tested snails survive. The latter method always gives a lower percentage if some snails die during the experiment. The estimated results are undoubtedly inaccurate, since we do not know whether any of the snails which died were infected.

Regardless of the method of calculation used, the results from the above authors all showed the same pattern of susceptibility, which was very low in the alpha, medium in the gamma and very high in the beta snails. Approximated susceptibility ratios of the alpha : beta : gamma races of *Tricula aperta* to *Schistosoma mekongi* were 1 : 5 : 2.4, respectively. This was calculated by using the numbers of the highest susceptibility rates of each race obtained from various authors, e.g., alpha = 12% from Liang & Kitkoon (1980), beta = 60% from my present data (Table 2) and gamma = 29% from Harinasuta et al. (1972). My results showed that the differences in susceptibilities of the three races to *S. mekongi* were also significant statistically (Table 3). I believe the other authors' results also would show a similar significance if they were analyzed statistically.

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EFFECTS OF SOME PHYSICO-CHEMICAL FACTORS ON THE SURVIVAL OF *BITHYNIA SIAMENSIS SIAMENSIS, RADIX RUBIGINOSA* AND *INDOPLANORBIS EXUSTUS*[1]

Y.P. Chitramvong[2], E.S. Upatham and N. Sukhapanth

ABSTRACT

Water temperature, salinity and pH were found to affect the survival of *Bithynia siamensis siamensis, Radix rubiginosa* and *Indoplanorbis exustus* in the laboratory. Of these three factors, hydrogen-ion concentrations exerted the least effect on the survival of the snails. The optimum pH values for all three species were between 6 and 7. When the range of pH was between 3 and 5, mean percentage mortality rates of all snails decreased as the pH values increased. When the range of pH was between 7 and 10, mean percentage mortality rates increased as pH values increased. The optimum temperatures to which snails were exposed for 24 hrs were 20-30°C. The temperatures above or below the optimum temperatures caused damage to physiological functions of snails and death, especially with prolonged exposure. The optimum concentrations of salinity to which all snails were exposed were between 0 and 200 mg/l. At a concentration of 6,400 mg/l, 100% mortality rates were obtained with *R. rubiginosa* and *I. exustus.*

INTRODUCTION

Bithynia siamensis siamensis Lea, *Radix rubiginosa* (Michelin) and *Indoplanorbis exustus* (Deshayes) are widely distributed in Thailand and serve as important intermediate hosts of parasitic trematodes. *B. s. siamensis* is the first intermediate host of *Opisthorchis viverrini* (Poirier), the liver fluke of man, cats and dogs (Wykoff et al., 1965). *R. rubiginosa* serves as intermediate host of a few flukes such as *Schistosoma incognitum* Chandler (the blood fluke of bandicoots and field rats; Lee & Wykoff, 1966), *Orientobilharzia harinasutai* Kruatrachue, Bhaibulaya & Harinasuta (the blood fluke of water buffaloes; Kruatrachue et al., 1965) and *Trichobilharzia maegraithi* Kruatrachue, Bhaibulaya & Harinasuta (the blood fluke of ducks; Kruatrachue et al., 1968). *Indoplanorbis exustus* is the intermediate host of *S. spindale* Montgomery, the blood fluke of water buffaloes and cattle (Harinasuta et al., 1965). The latter snails also can act as the first and second intermediate hosts of *Hypodereum conoideum* (Bloch) and *Echinostoma* spp., the intestinal flukes of ducks (Yokogawa et al., 1965) and rats and ducks (Bhaibulaya et al., 1964), respectively. These flukes are also infective to man.

In natural environments, temperature is usually considered as the most important ecological factor influencing the distribution of animals (Gunter, 1957). The influence of temperature on the biology and survival of various species of freshwater mollusks has been reported (e.g., see Sturrock, 1970; Sturrock & Sturrock, 1972; van der Schalie & Berry, 1973). Castagna & Chanley (1973) indicated that salinity affected growth, reproduction and distribution of marine bivalves in Virginia. Harrison & Agnew (1962) found that some temperate species of mollusks appear to prefer slightly acidic water (pH 6.0-6.9) while others prefer alkaline water (pH 8.5).

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This study reports on the effects of temperature, pH and salinity on the survival of *Bithynia siamensis siamensis, Radix rubiginosa* and *Indoplanorbis exustus*.

MATERIALS AND METHODS

Bithynia siamensis siamensis (10.5 mm), *Radix rubiginosa* (12.5 mm) and *Indoplanorbis exustus* (12.5 mm) were obtained from ponds or roadside ditches in Bangkaen District, Bangkok, Thailand. In the laboratory, they were kept in aquaria containing aged tap water for two days prior to the experimentation. *R. rubiginosa* and *I. exustus* were fed lettuce and fish food, whereas *B. s. siamensis* were fed with synthetic food (Sumethanurugkul, 1970)*. For each experiment, a total of 960 active snails was used, and each experiment was replicated once. Snail mortality rates were assessed 48 hrs after exposure.

Water temperature

The experiment was performed in two series. Firstly, the snails were exposed in various temperatures ranging from 5-40°C at 5°C intervals for 24 hrs and, secondly, they were exposed for seven days. In each series, 20 snails of each species were placed separately in 250 ml beakers containing aged tap water. For the seven-day exposure period, each species of snails was fed with its food as described above and the water was changed every two days to remove snail metabolic wastes. The beakers were covered with pieces of cotton gauze to prevent snails from crawling out.

At water temperatures of 5°, 10°, 15° and 20°C, the beakers containing snails were placed in low-temperature incubators; at 25°C, they were placed in an air-conditioned room; and at 30° (control temperature), 35° and 40°C, they were placed in waterbaths.

Salinity

A graded series of seven sodium chloride (NaCl) concentrations were used, each with a two-fold increase in concentration, ranging from 100 to 6,400 mg/l. These concentrations were prepared with deionized water. Sixteen 250 ml beakers were used for containing each species of snails: 14 for experimental snails and two for control snails. Each beaker contained 20 snails. Snails were placed in various sodium chloride concentrations for 24 hrs at room temperature (30°C).

Hydrogen-ion concentration

Snails were exposed to pH values ranging from 3 to 10, at one pH value intervals. Using deionized water, the acidic pH values were adjusted with 0.1 N hydrochloric acid and the alkaline pH values with 0.1 N sodium hydroxide. The deionized water had a pH value of 7.0. All pH values were measured with a radiometer before and after the exposure period, which lasted for 24 hrs.

Sixteen 250 ml beakers were used for each snail species. Each beaker contained 20 snails.

RESULTS

Water temperature

The results of the 24-hr exposure period are shown in Fig. 1. As water temperatures increased from 5° to 15°C, the mean percentage mortality rates of snails decreased. The best survival temperatures for all snails fell between 20° and 30°C. At high water temperatures, mean percentage mortality rates of snails increased sharply, from 5-10% at 35°C to 90-95% at 40°C. *Indoplanorbis exustus* exhibited the highest tolerance to lower water temperatures, followed by *Bithynia siamensis siamensis* and *Radix rubiginosa*.

The results of the seven-day exposure period are shown in Fig. 2. Snail mortality rates exhibited similar patterns to those of the 24-hr exposure period. But, the rates were higher with the longer exposure period, and these could be seen more clearly at low temperatures.

Salinity

The effects of sodium chloride on snails are shown in Fig. 3. Snail mortality rates increased with increasing concentrations of sodium chloride. At concentrations lower than 400 mg/l,

*Synthetic snail food: powdered rice (21g), powdered dried leaves of *Leucaena glaura* (Leguminosae) (21 g), powdered milk (7 g), miltivitamin complex (3 g), $CaCO_3$ powder (1 g), agar (0.1 g) and distilled water (400 ml).

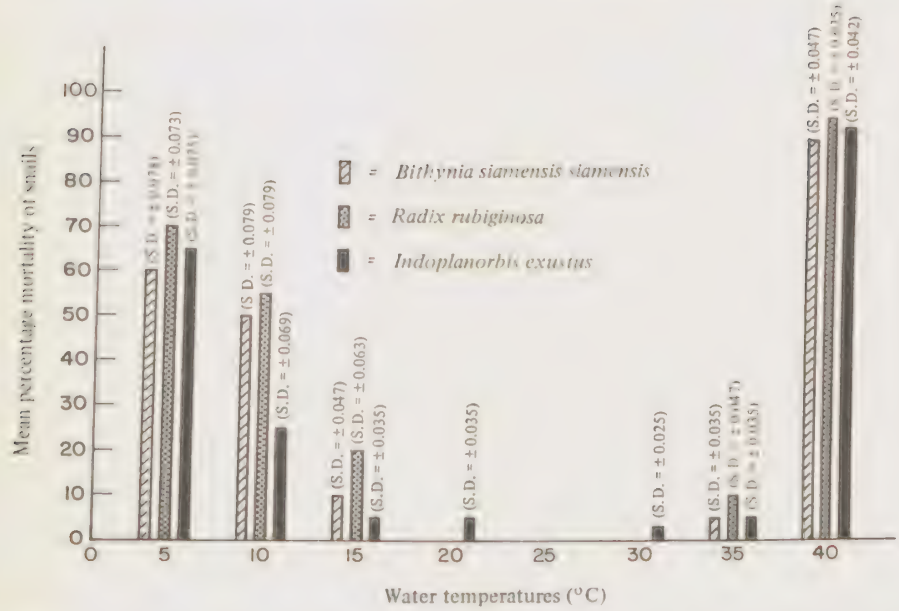

FIG. 1. Effects of water temperatures on *Bithynia siamensis siamensis, Radix rubiginosa* and *Indoplanorbis exustus*, exposed for 24 hrs.

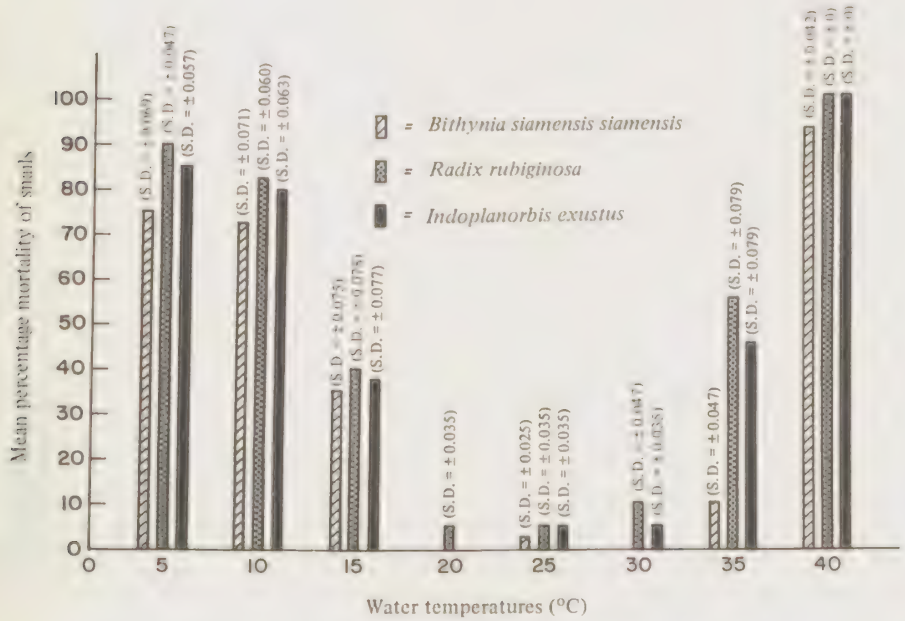

FIG. 2. Effects of water temperatures on *Bithynia siamensis siamensis, Radix rubiginosa* and *Indoplanorbis exustus*, exposed for seven days.

snail mortality rates were lower than 20%. At 6,400 mg/l, mortality rates of *Radix rubiginosa* and *Indoplanorbis exustus* reached 100%, whereas that of *Bithynia siamensis siamensis* was

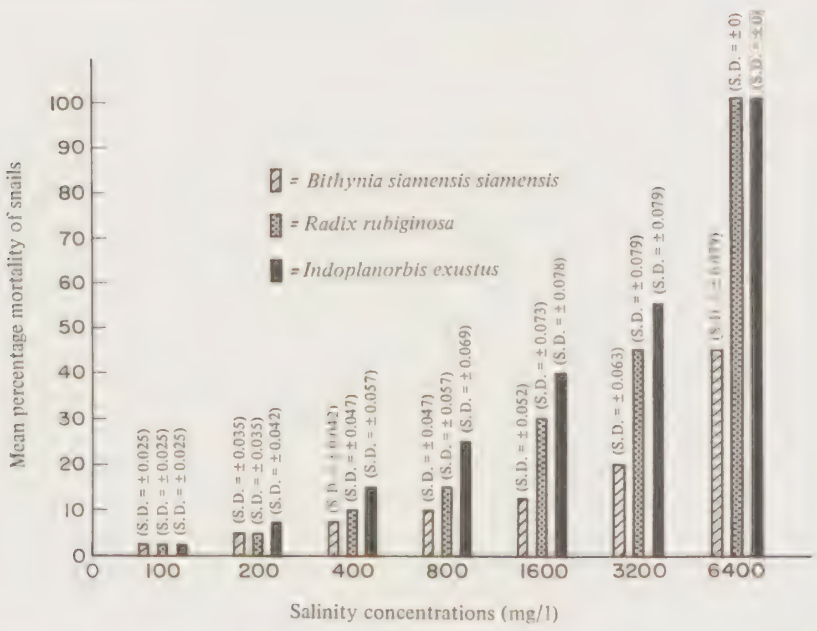

FIG. 3. Effects of salinity on *Bithynia siamensis siamensis*, *Radix rubiginosa* and *Indoplanorbis exustus*, exposed for 24 hrs.

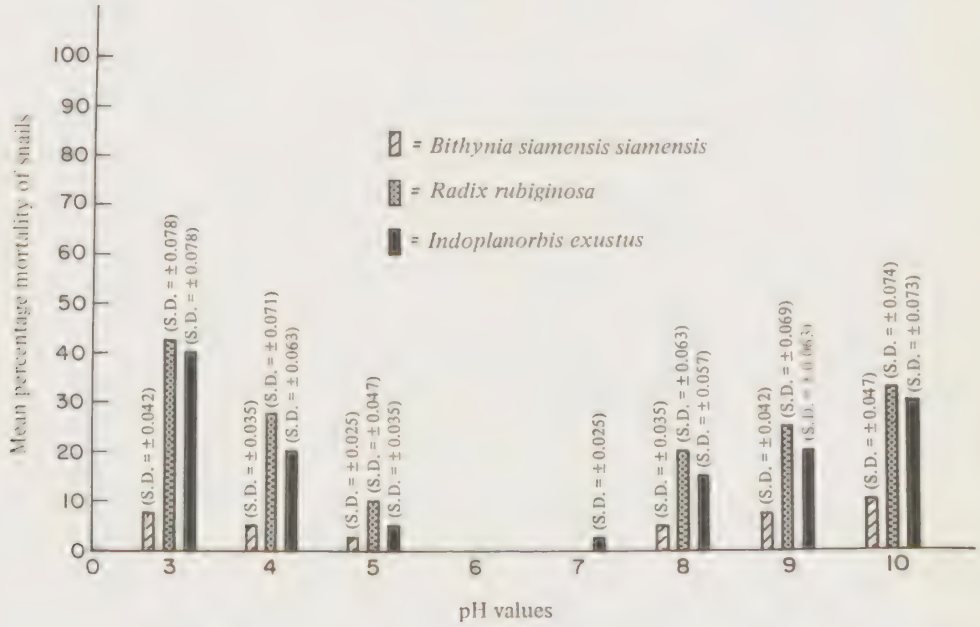

FIG. 4. Effects of pH values on *Bithynia siamensis siamensis*, *Radix rubiginosa* and *Indoplanorbis exustus*, exposed for 24 hrs.

only 45%. *B. s. siamensis* was least affected and *I. exustus* and *R. rubiginosa* were most affected by sodium chloride.

Hydrogen-ion concentration

The effects of pH values are shown in Fig. 4. At pH values from 3 to 5, snail mortality rates decreased as pH values increased, whereas at pH values from 8 to 10, the rates increased with increasing pH values. Snails could tolerate pH 6 and 7 best.

Bithynia siamensis siamensis was least affected and *Radix rubiginosa* and *Indoplanorbis exustus* were most affected by pH of the water.

DISCUSSION

Each of the physico-chemical factors tested – water temperature, salinity and pH – was found to affect the survival of *Bithynia siamensis siamensis*, *Radix rubiginosa* and *Indoplanorbis exustus*.

Although snails are ectothermic animals adapting to the variation of a thermally unstable environment, there is a limit to their ability to adapt to changes in the environment (Weiser, 1973). Sturrock (1970) found that temperatures above 41°C caused complete mortality in *Biomphalaria glabrata* (Say). A rise in temperature causes the metabolism to accelerate and harmful metabolites to accumulate in ectothermic animals (Weiser, 1973). In addition, it also promotes membrane permeability which may disturb the distribution of ions and small molecules on either side of the membrane. This rise in temperature to 40°C may, therefore, have resulted in the death of nearly all snails of all species during the 24-hr exposure period, and of all snails except for a few *Bithynia siamensis siamensis* during the seven-day exposure period. A fall in temperature from 15° to 5°C apparently disturbed certain aspects of the snails' physiological functions, and this may have been associated with slow dehydration of the cells (Weiser, 1973). He explained that this was because the physiological functions depended on the supply of a minimum number of molecules per unit time. In the case where the speed of reaction was below the critical value, the energy was too low to be transported to supply the animals' systems. Hence, the entire physiological functioning would stop and cause death. The results of this study indicated that all snails could tolerate lower temperatures (5°, 10°, 15°C) better than extremely high temperature (40°C) during the 24-hr exposure period.

Tolerance of snails to salinity varied greatly among species at concentrations higher than 400 mg/l. At concentrations ranging from 800 to 3,200 mg/l, *Radix rubiginosa* was more tolerant than *Indoplanorbis exustus*. This probably is because *R. rubiginosa* may be able to excrete ions from its tissues faster. However, it is doubtful that they could survive in sodium chloride concentrations up to 3,200 mg/l for an extended period of time. The ability of *Bithynia siamensis siamensis* to survive the highest concentration, which killed all of the other species, may be due to its ability to prevent an unfavorable chemical from entering the body by closing its operculum rather than to its physiological adaptation.

Castagna & Chanley (1973) found that temperature also may influence the degree of toxicity of salinity. In this study, however, it is likely that different salinity concentrations alone affected the survival of the snails because the snails were maintained near the optimum temperatures.

In natural habitats, snails can survive and disperse widely at pH 7.4. Harrison & Agnew (1962) found that some temperate species of freshwater molluscs, such as *Radix natalensis* (Krauss), *Pseudosuccinea columella* (Say) and *Bulinus tropicus* (Krauss), appeared to prefer alkaline water (pH 8.5). In this study, snails were slightly more tolerant in acidic water, at pH 4-6, than in alkaline water, at pH 8-10.

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BEHAVIOURAL STUDIES ON THE NATURE OF STIMULI RESPONSIBLE FOR TRIGGERING MUCUS TRAIL TRACKING BY *BIOMPHALARIA GLABRATA*

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ABSTRACT

Many species of aquatic snail follow mucus trails. *Biomphalaria glabrata*, a freshwater planorbid, for example, will follow trails laid by conspecifics, but not those of another freshwater species, *Lymnaea stagnalis*. In addition, the trails of *B. glabrata* are only effective in triggering tracking behaviour for about 20-30 min after they have been laid. In this paper, further experiments aimed at elucidating the possible nature of the stimuli in mucus which is responsible for triggering trail following, and for determining the specificity of behavioural response observed, are described. It is concluded that metabolic factors released in the mucus are involved.

INTRODUCTION

Mucus trail following is a common phenomenon amongst aquatic molluscs, and, although often restricted to trails left by conspecifics or a small number of related species, little attention has been paid to the nature of the stimuli underlying the response (see Paine, 1963; Peters, 1964; Gonor, 1965; Cook, A., et al., 1969; Cook, S.B., 1969; Crisp, 1969; Wells & Buckley, 1972; Hall, 1973; Townsend, 1974b; Cook, A., 1977; Chase et al., 1978; Trott & Dimock, 1978).

Recently, Townsend (1974b) has demonstrated that *Biomphalaria glabrata* (Say), a freshwater planorbid snail found in South America and the Caribbean, will follow trails laid by conspecifics, but not those made by another freshwater species, *Lymnaea stagnalis*. In addition, although the mucus trail persists for many hours (Bousfield, unpubl. observ.), tracking behaviour is only triggered by trails aged less than 30 min (Townsend, 1974b).

The laying of a mucus trail is an essential concomitant of movement for most gastropod species, since it transforms ciliary motion on the base of the foot into locomotion of the whole animal. There is considerable evidence to suggest that the physical properties of mucus affect its rate of transport across ciliated surfaces. Thus the speed of movement on a trail might be radically altered by species differences, or temporal changes in the viscosity, or elasticity of the mucus beneath the snail (see Hyman, 1967; Blake & Sleigh, 1974; King et al., 1974; Trueman, 1975; Meyer, 1976). This, in turn, might influence the distance for which snails would follow different trails.

A number of recent studies indicate that chemical factors are involved in inducing trail following. It is known that snails release a variety of metabolites in their mucus (Wilson, R.A., 1968), and amongst these are compounds known to be potent snail attractants (Uhazy et al., 1978; Thomas & Assefa, 1979; Thomas et al., 1980; Thomas et al., 1981). Thus different concentrations of metabolites in the trails laid by different species of snail and diffusion might account for the observed specificity of mucus trail tracking behaviour.

In the present paper, experiments are described which provide some insight into the relative importance of physical and chemical cues in triggering the mucus trail tracking behaviour of *Biomphalaria glabrata*. More specifically, the following questions have been asked.

1. Will this snail follow trails laid by species more closely related than *Lymnaea stagnalis*? This provides basic information on the taxonomic distribution of attractive factors.

2. Is tracking behaviour affected by the metabolic state of the marker snail? The effects of changes of diet, starvation, and anoxia have been examined. Are these effects restricted to trails laid by conspecifics?

3. Could the gradual waning in trail activity be due to diffusion of a chemical into the surrounding water?

4. Are any of the changes in degree of mucus trail tracking noted above accompanied by changes in speed of movement of the tracking snail? This would provide evidence for or against the role of changes in physical properties of mucus playing a dominant part.

METHODS

General

Reproductively mature snails were used exclusively throughout these experiments. The individual *Biomphalaria glabrata* used weighed approximately 400 mg (a typical standard deviation on an experimental population was 70 mg). Individuals of the other species used were selected so as to have foot widths similar to *B. glabrata*, as this facilitated the measurement of the extent of trail overlap.

Biomphalaria pfeifferi (Krauss), *B. tenagophila* (Orbigny), *Planorbella (Seminolina) duryi* (Menke), *Physella waterlotti* (Germain), *Physella acuta* (Draparnaud) and *Lymnaea stagnalis* (Linnaeus) were all taken from laboratory cultures fed with lettuce (Thomas, 1973). *Planorbis planorbis* (Linnaeus), *L. (Radix) pereger* (Müller) and *L. (Stagnicola) palustris* (Müller) were collected from the Lewes Brooks area in East Sussex (National Grid Reference TQ4008), as were the aquatic plants, *Apium nodiflorum* (Linnaeus) (Umbelliferae) and *Rorippa nasturtium-aquaticum* aggregation (Cruciferae), used in the diet experiments.

Each snail species was kept in small plastic buckets at densities of 20/l in water of controlled ionic composition (Thomas, 1973; Bousfield, 1978) for a period of one week. These were maintained at 26°C under a constant 12 hr light/12 hr dark regime. Each day, fresh water and food in the form of 0.1 g lettuce per snail per day were provided, except in the experiments where three separate populations were fed on diets of lettuce, *Apium* and *Rorippa* respectively.

The experimental snails were placed in fresh medium without food at densities of 20/l for one hour before testing. Snails treated in this way tended to produce trail patterns which were less convoluted than those of snails allowed to feed prior to testing. For example, if deprived and fed snails were placed individually in the center of an 8 cm radius circle, they reached the circumference after moving, on the average, 8.13 ± 1.80 cm and 18.05 ± 8.58 cm respectively ($\bar{x}$ ± S.D., n = 20 in each case). This treatment therefore made the analysis of overlap much simpler. Individual snails were not used more than once each day in these experiments.

Assay apparatus and procedure

Full details of the test arena have been given elsewhere (Bousfield, 1978; 1979). Briefly, it consisted of a cylindrically symmetric perspex container, of radius 23 cm, fitted with a removable glass floor which was thoroughly cleaned between trials. During the test it was filled to a depth of 1.5 cm with water at 26°C. For some experiments, a current was required to act on the marker trail before the insertion of the tracker snail. This was achieved using the air jet system described by Bousfield (1978, 1979). Flow velocities 5 mm above the bottom averaged 5 mm/sec under these conditions (Bousfield, 1979). In all experiments, the arena was diffusely illuminated from above, and snail movement monitored from below using a closed circuit television system.

The test procedure was as follows. A moving snail was removed gently from its container and placed at the center of an 8 cm radius circle drawn on the glass floor of the arena. The subsequent movement of this 'marker' snail was recorded by tracing the area covered by the foot on the screen of a video monitor until it first reached the edge of the 8 cm radius circle. This snail was then removed and a second 'tracker' snail introduced onto the beginning of the marker trail with its shell oriented in the same direction as that of the marker snail. Again, movement was recorded until this snail too had reached the boundary. In addition, the timing of the introduction and removal of the two snails was recorded so that average snail speed and trail age could be assessed. In all experiments other than those designed to look specifically at the waning effect, the time for a complete trial was limited to 10 min. Thus, if tracker snails had not reached the boundary 10 min after insertion of the marker snail, the trial was disregarded.

Statistics

Each trial, consisting of one marker and one tracker snail, generated one or more trail 'overlap'. An overlap was defined as any length of tracker trail which touched, or which partially or wholly covered, the marker trail. Overlaps generated by a tracker snail which doubled back over its own trail and, at the

same time, overlapped a portion of marker trail were ignored, as was overlap generated by the first 1.5 cm of tracker trail. This portion was excluded because, by the nature of the assay, it would in the majority of test and control cases result in overlap. Individual overlaps and total trail lengths were measured by tracing trail patterns using a cartographers curvimeter.

Since tracker snails were started from the same initial position, and with the same shell orientation as marker snails, control overlap values could be obtained by superimposing marker trails (in cases where both snails were of the same species and had received identical pretreatments) or by running a number of 'sham tracker' snails in the absence of markers and superimposing their trails upon those of the marker snails. Since the marker and tracker trails could be permuted, relatively few 'single tracker' trials were required.

Average speeds of movement were calculated by dividing trail lengths by the total laying time. The average age of a marker trail followed by the tracker snail was taken to be the quantity $\frac{1}{2}(t_1 + t_3) + t_2$, where t_1 and t_3 were the times taken to lay the marker and tracker trails respectively and t_2 was the time interval between the removal of the marker and insertion of the tracker snail.

The distribution of individual overlap lengths provides a measure of the likelihood with which a snail will continue to follow a trail once one has been encountered. It does not give an indication of the total length of a marker trail likely to be followed, since in many cases tracker snails moved off a trail they were following only to move back onto it a centimeter or so further on. It is probable that under these circumstances the tracker snail was still aware of the exact location of the marker trail, since the tentacles are known to direct currents of water from their tips onto chemoreceptor sites at their base (Townsend, 1974a). However, since, for this brief period, the overlap criteria described above were not satisfied, the two sections of overlap were regarded as being separate. Where comparisons have been made between different data populations, non-parametric statistics have been used exclusively (Siegel, 1956). This was calculated by dividing the sum of the individual overlap lengths by the total tracker trail length. In some instances, as described below, it was useful to estimate the proportion of a total tracker trail which was overlapping a marker trail.

RESULTS

Species specificity

The degree to which *Biomphalaria glabrata* followed trails laid by individuals belonging to nine other species of snail was tested in two series of experiments. The results of these experiments are shown in Table 1. Townsend's (1974b) conclusion regarding the absence of significant following of trails laid by *Lymnaea stagnalis* is confirmed; however, *B. glabrata* will follow trails left by other species of snail. It is of interest that, with one exception, these species are also planorbids. Most marked was the following of trails laid by *Planorbella (Seminolina) duryi* and *B. pfeifferi*. The two remaining planorbids tested, *B. tenagophila* and *Planorbis planorbis*, produced trails which were also followed, albeit to a much less significant extent. Mean individual overlap lengths obtained using the physid *Physella acuta* were also just significantly different from control values. In contrast, no significant differences were noted for *Physella waterlotti* or the three lymnaeid species tested, *L. stagnalis*, *L. (Radix) pereger* and *L. (Stagnicola) palustris*.

The frequency distributions for individual overlaps generated when *Biomphalaria glabrata* follows trails laid by conspecifics are contrasted with those obtained with *Lymnaea (Radix) pereger* trails in Fig. 1. It can be seen that both the control distributions contained overlaps of predominantly less than 1 cm, as did the test distribution obtained with *L. (R.) pereger* (>75% in each case). When the marker snail was *B. glabrata*, however, overlaps of up to 8 cm were recorded.

As has already been mentioned in the Methods section, the mean individual overlap is considerably less than the mean total overlap obtained in a single trial. For *Biomphalaria glabrata* marker snails, for example, total overlap values of over 20 cm could be obtained. The significance values are not altered, however, if mean total instead of mean individual overlap is used as a statistic (Bousfield, unpubl. observ.).

TABLE 1. Overlap values obtained for *Biomphalaria glabrata* following trails laid by various species of snail.

Marker species	Mean individual overlap (cm)		P-value +
	Test	Control	
Planorbidae			
Biomphalaria glabrata[1]	3.81(24)*	0.77(37)*	<0.001
Biomphalaria glabrata[2]	2.46(62)	0.51(61)	<0.001
Biomphalaria pfeifferi[1]	3.20(30)	0.47(132)	<0.001
Biomphalaria pfeifferi[2]	2.77(50)	0.50(109)	<0.001
Biomphalaria tenagophila[1]	1.19(29)	0.25(158)	<0.05
Biomphalaria tenagophila[2]	1.24(29)	0.74(116)	N.S.
Planorbella (Seminolina) duryi[1]	2.30(15)	0.39(103)	<0.001
Planorbella (Seminolina) duryi[2]	3.07(13)	0.41(62)	<0.001
Planorbis planorbis[2]	1.72(25)	0.62(77)	<0.05
Lymnaeidae			
Lymnaea stagnalis[1]	0.77(22)	0.55(48)	N.S.
Lymnaea (Radix) pereger[2]	1.33(24)	0.76(119)	N.S.
Lymnaea (Stagnicola) palustris[2]	0.98(12)	0.64(54)	N.S.
Physidae			
Physella waterlotti[1]	0.41(10)	0.22(150)	N.S.
Physella acuta[2]	1.23(26)	0.46(106)	<0.05

+ = Mann-Whitney U^2 test; [1] = experiments conducted Summer 1976; [2] = experiments conducted Summer 1977; * = number of observations, given in parentheses; N.S. = not significant.

Possible influence of diet

Three groups of experimental snails were raised for one week prior to testing on diets consisting entirely of either lettuce, *Apium nodiflorum* or *Rorippa nasturtium-aquaticum*. The latter two species were chosen because, although they are known to be capable of sustaining snail growth and reproduction (Bousfield, unpubl. observ.), they differ considerably in terms of their 'secondary' chemical composition (Harbourne, 1977).

The results of these experiments are shown in Table 2i. Although the mean values for individual overlaps recorded when *Biomphalaria glabrata* followed *Rorippa*- and *Apium*-fed

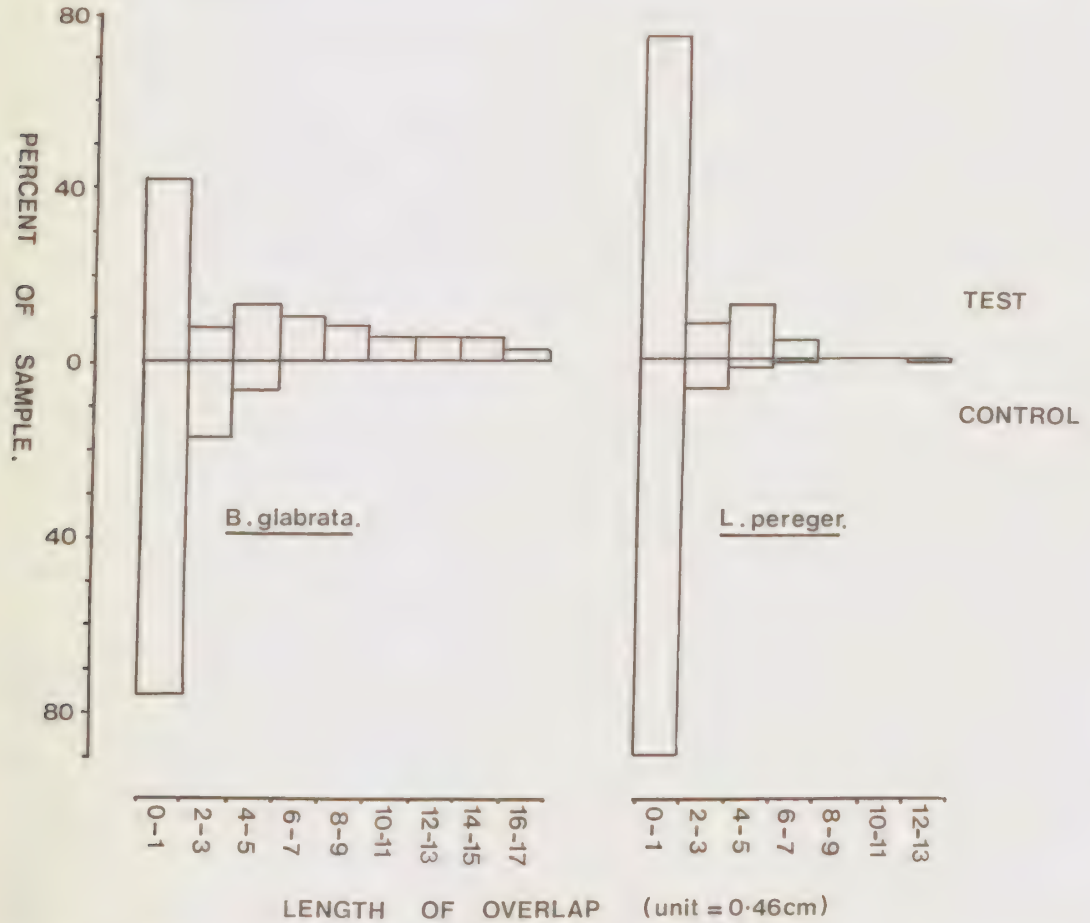

FIG. 1. Histograms representing the distribution of individual overlap lengths recorded in experiments using *Biomphalaria glabrata* (left) and *Lymnaea (Radix) pereger* (right) as marker snails. In each case, the top histogram represents 'test' values, while the bottom one is for 'controls'.

conspecifics were slightly less than those observed using lettuce-fed marker snails, this difference was not significant (Mann-Whitney test; Siegel, 1956).

In contrast, Table 2ii shows that the mean overlap obtained for marker snails which had been starved for 12 hours prior to testing was significantly less than the mean overlap for lettuce-fed snails ($p<0.05$: Mann-Whitney test). During the same experiments, some of the snails which had been deprived of food were placed in water freed of gas (by boiling and storage under vacuum) in a stoppered bubble-free bottle for a period of 2-3 hrs before testing to render them anoxic. This treatment resulted in a dramatic increase in the individual overlaps observed when 'normal' snails followed their trails (see Table 2ii). Indeed, these values were higher than any others recorded during the course of the experiments.

This period of anoxia was, however, not without obvious effects on the behaviour of the snails. Their mean speed of movement was considerably reduced when compared to that of marker snails which previously had been starved or had been feeding, although the speeds of the tracker snails were not affected dramatically (see Table 2iii).

Since the evidence presented so far suggests different species of snail produce trails which have different levels of ability to stimulate tracking and because, in the case of *Biomphalaria*

TABLE 2. Effects of diet and starvation on marker trail attractiveness, and of anoxia and starvation on speeds of marker and tracker snails.

i) Effect of diet on marker trail attractiveness

Marker diet	Mean individual overlap (cm)	Quartiles	P-value+
Lettuce	3.09(21)*	1.35-4.50	
Rorippa	2.58(15)	0.67-3.15	N.S.
Apium	2.61(26)	0.56-4.39	N.S.

ii) Effect of starvation on marker trail attractiveness

Previous condition of marker	Mean individual overlap (cm)	Quartiles	P-value+
Feeding	2.65(17)*	0.92-4.14	
Starved	1.54(17)	0.42-1.38	<0.05
Starved + anoxic	6.44(10)	2.86-9.09	<0.05

iii) Effect of starvation of marker snail on speeds of marker and tracker snails

Previous condition of marker	Mean speed of marker (cm/min)	Mean speed of tracker (cm/min)	P-value+
Feeding	5.10	5.27	N.S.
Starved	4.48	4.68	N.S.
Starved + anoxic	1.85	4.07	<0.01

* = number of observations, given in parentheses; + = Mann-Whitney U^2 test; N.S. = not significant.

In i) and ii), p-values are for comparisons between lettuce-fed and feeding snails respectively. In iii), the comparisons are between the mean speeds of movement of tracker and marker snails.

glabrata, brief periods of anoxia radically increase the effectiveness of the mucus produced, it was interesting to consider whether *B. glabrata* would follow trails laid by anoxic snails of a species which previously was ineffective. Consequently, trails laid by normal and anoxic (1-2 hrs) *Lymnaea stagnalis* were compared using lettuce-fed *B. glabrata* trackers. The results of these experiments are given in Table 3 and show that a brief period of anoxia does indeed lead to trails being produced which are followed to a significant degree by *B. glabrata*. Thus physiological factors can profoundly influence the effectiveness of mucus in inducing trail following, even for species which do not normally produce mucus trails followed by *B. glabrata.*

TABLE 3. The effect of anoxia on mucus trails laid by *Lymnaea stagnalis* and the trail following behaviour of *Biomphalaria glabrata*.

Marker snail	Mean individual overlap (cm)	Quartiles	P-value+
Normal *Lymnaea stagnalis*, controls	0.41(29)*	0.00-0.46	
Normal *Lymnaea stagnalis*, test	0.33(11)	0.00-0.46	N.S.
Anoxic *Lymnaea stagnalis*, test	2.21(11)	0.69-3.22	<0.001

* = number of observations, given in parentheses; + = Mann-Whitney U^2 test; N.S. = not significant.

Both p-values are for comparisons with controls.

Waning period – the role of diffusion

The trails laid by *Biomphalaria glabrata* cease to be effective in eliciting tracking behaviour after a period of 10-30 min (Townsend, 1974b).

Two series of experiments were designed to examine whether a diffusion process was responsible for limiting the length of time that trails remained attractive to conspecifics. In the first group, the effect of separating the foot of the tracker snail from the marker trail using a thin permeable barrier was examined. This was achieved using a sheet of Tygan netting with a thickness of between 500 and 750 μ and 20 x 20 (approximately 1 x 1 mm) mesh size. If trail following could still be demonstrated when the mesh covered the marker trail, then this would be good evidence that the behaviour could be triggered by diffusing chemicals. In order to allow for the re-establishment of chemical gradients following their disruption by placement of the mesh over the marker trail, a period of between 5 and 10 min was allowed before the tracker snail was placed at the starting point. In addition to the usual control experiment, a further two were run to check whether trails laid on mesh tracking still occurred and, if so, whether they were affected by the physical disruption caused by moving and replacing the mesh in water. The results of the experiments can be found in Table 4. Mean individual overlap length was found to be statistically significantly greater than controls for the standard assay, in which both snails moved over a glass substrate, and for the two situations in which both snails were moving on mesh. Indeed, the mesh substrate appeared to increase greatly the tendency for the snails to follow trails despite even the disruption caused by the temporary removal of the marker trail. In contrast, for the situation in which the tracker snail was separated from the mucus trail of the marker snail, the mean individual overlap, although twice the control value, was not significantly different when compared to values obtained for sham tracker snails.

It is possible that the rough surface texture of the mesh was an important factor in these experiments. For example, it is probable that the surface was difficult for the snails to adhere to, since the area of contact between the foot and substrate was reduced greatly. Most freshwater pulmonates often become positively buoyant, particularly after taking in air at the surface of the water (Jones, 1975), and this is certainly true for *Biomphalaria glabrata*

TABLE 4. The effect of mean overlap values of separating test and control trails with a thin Tygan mesh.

Test situation	Mean individual overlap (cm)	Quartiles	P-value+
Control	0.70(28)*	0.44-0.88	
Both snails on glass	2.97(17)	0.44-5.28	<0.05
Both snails on mesh	4.51(8)	0.44-7.26	<0.01
Tracker snail on mesh overlay	1.20(23)	0.44-0.88	N.S.
Both snails on mesh, mesh removed between marker and tracker trials	3.90(15)	1.54-6.16	<0.001

* = number of observations, given in parentheses; + = Mann-Whitney U^2 test; N.S. = not significant.

All p-values are for comparisons with controls.

(Bousfield, unpubl. observ.). The mucus film, in addition to translating the beat of the pedal cilia into bodily locomotion, clearly also serves to promote adhesion between the foot and the surfaces over which the snails move. Perhaps, under circumstances in which adhesion is made difficult, chemical cues are ignored in preference to the ease of movement on a pre-formed mucus trail. To test this hypothesis, trails were laid on Tygan mesh using *Lymnaea stagnalis* as marker and *B. glabrata* as tracker. The results of these experiments are shown in Table 5. However, even under these circumstances *B. glabrata* would not follow trails laid by *L. stagnalis*, confirming the observation made earlier that the presence of a mucus trail alone is not sufficient stimulus to trigger trail following behaviour.

A second series of experiments was performed to investigate whether diffusion processes were responsible for generating the waning effect. If it is hypothesized that diffusion across the water-mucus interface is the limiting factor in determining the duration of activity in trails, then the presence of a current should reduce the waning period considerably.

TABLE 5. The effect of the presence of Tygan mesh on the trail following behaviour of *Biomphalaria glabrata* on mucus laid by *Lymnaea stagnalis*.

Marker snail	Tracker snail	Mean individual overlap (cm)	P-value+
Biomphalaria glabrata	*Biomphalaria glabrata*, control	0.46(17)*	
Biomphalaria glabrata	*Biomphalaria glabrata*, test	3.60(10)	<0.01
Lymnaea stagnalis	*Biomphalaria glabrata*, control	0.46(23)	
Lymnaea stagnalis	*Biomphalaria glabrata*, test	0.86(17)	N.S.

* = number of observations, given in parentheses; + = Mann-Whitney U^2 test; N.S. = not significant.

Each p-value for comparison with appropriate control.

A water current was generated in an arena containing trails deposited by a marker snail by using a system of air-jets (see Methods; also see Bousfield, 1978, 1979). After an interval of approximately 3, 15 or 30 min, the flow was stopped and a tracker snail introduced onto the start of the marker trail. The overlaps produced by these snails were compared with those of a series of snails in which the introduction of the tracker snail had been delayed by similar amounts of time but in the absence of current. The results of this series of experiments are shown in Fig. 2. The overlaps produced by the control snails (snails followed trails which had not been subject to flow) showed the characteristic decay in mean length described previously by Townsend (1974b). In these experiments, the half-life of a trail, based on measurements of mean individual overlap, was estimated to lie between 15 and 20 min. However, although the mean overlap lengths produced by test snails were in all three cases less than those produced by controls, this difference was very small and statistically insignificant (Mann-Whitney test, $p > 0.1$ in all cases).

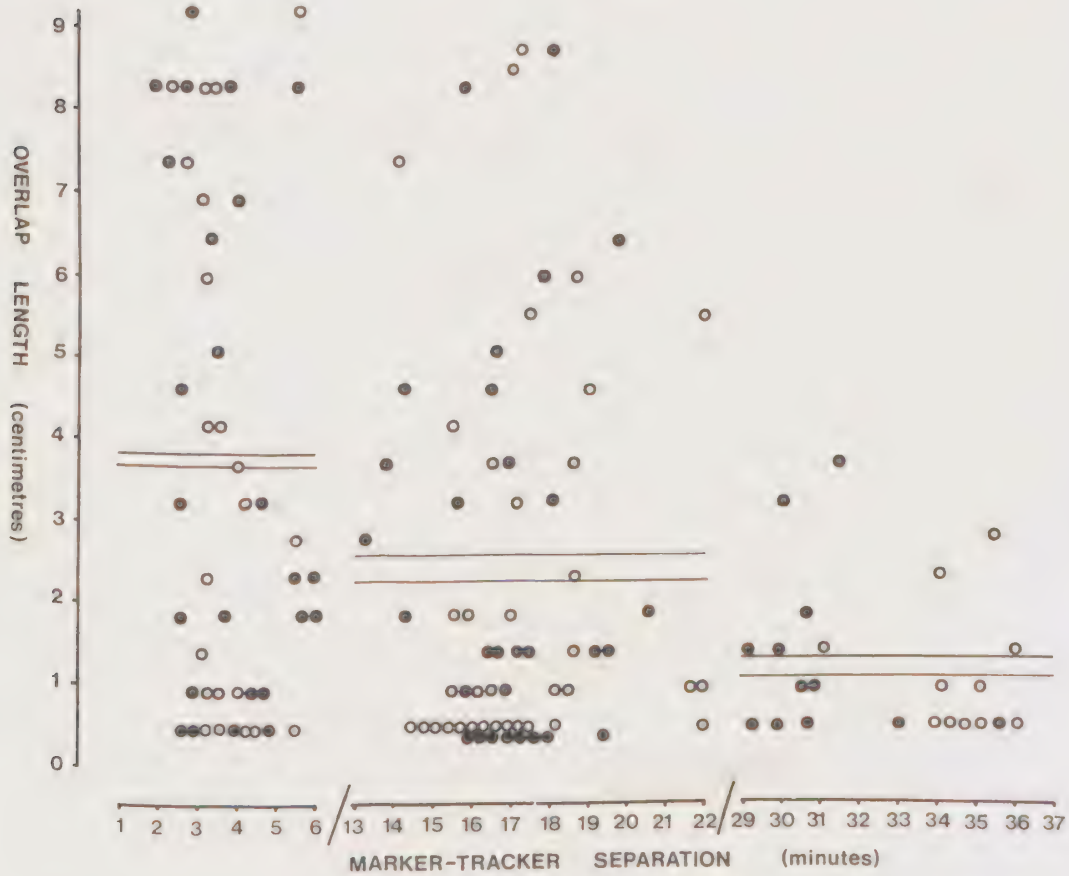

FIG. 2. The distribution of overlap lengths recorded for *Biomphalaria glabrata* following trails aged for different periods of time and made by conspecifics. The filled circles represent data obtained in the normal manner, while the open circles represent data which involved subjecting the marker trail to current during the period before insertion of the tracker snail. The horizontal lines represent mean values obtained in cases where the average separation was approximately 3, 15 and 30 min. In each case, the upper line represents filled circle data. There was no statistically significant difference at any of the three marker-tracker separations.

One possible explanation for the gradual reduction in trail following is that it is caused by changes in the physical structure of the mucus. At one extreme, it can be hypothesized that the mucus gel gradually breaks up and goes into solution during the waning time. This can be tested by using simple techniques to visualize the trail and so check that it is still present at times far in excess of those at which trail following becomes undemonstrable. Alternatively, more subtle changes in the physical properties of the gel may occur. Since the mucus trails could be observed for over 6 hr after they had been laid, it was assumed that dissolution was not an important factor involved in the waning process.

For gastropods which rely on ciliary movement within a mucous film for locomotion, speed of movement may be critically dependent on the visco-elastic properties of the foot mucus (Blake & Sleigh, 1974). If the properties of the secreted gel change with time, as has been observed in some 'in vitro' preparations of human mucus secretions (Sadé et al., 1975; Creeth et al., 1977), then velocity of movement of snails following trails of different ages might be a useful way in which to monitor these changes indirectly. However, the data presented in Table 6 shows that snails following trails 3 min old (i.e., over 90% of the length of the tracker trail was involved in overlap) or 15 min old (over 50% involvement) move at speeds no different than those of snails which did not follow trails (mean total overlap less than 20% of the length of the tracker snail). This data also should be compared with the effects of starvation and anoxia on trail following (Table 2iii) where, despite large differences in mean overlap, no comparable changes in snail speed were observed. No statistically significant differences were found either when the speeds of movement of test and control snails shown in Table 1 were compared.

TABLE 6. Average speeds of movement for *Biomphalaria glabrata* following different-aged trails laid by conspecifics.

Average delay between marker and tracker snails	Mean speed of movement (cm/min)		P-value+
	Test†	Control†	
3 min	6.31(16)*	6.48(5)	N.S.
15 min	4.16(11)	5.60(18)	<0.05

+ = Mann-Whitney U^2 test; † = test snails were those which overlapped marker trails for over 90% (3 min delay) or over 50% (15 min delay) of their total length; control values were taken from snails for which the proportion of overlap did not exceed 20%; * = number of observations, given in parentheses. The difference in mean velocity apparent for the two delay groups probably can be accounted for by differences in the temperature of the test medium (see Methods; also see Jones, 1975).

DISCUSSION

The structure and composition of mucus

Mucus consists typically of about 1% by weight of salts and other dialysable components, 0.5-1% of free protein, a similar proportion of carbohydrate-rich glycoprotein, and 95% or more water (Wilson, R.A., 1968; Creeth et al., 1977; Whitehead, 1978). The macromolecular glycoproteins cross-link to form an extended gel-type network possessing viscosity and

elasticity (Creeth et al., 1977; Clamp et al., 1978). In addition to these important macromolecular structural components, many low molecular weight metabolites have been found in mucus of pulmonates (Wilson, R.A., 1968; Simpson and Chamberlain, pers. comm.). Thus, despite the small amount of material involved, it is clear that mucus possesses a wide variety of physical properties and chemical components, each of which may, to a greater or lesser extent, be responsible for influencing trail tracking behaviour. The following discussion indicates that chemical, as opposed to physical factors, play a dominant role in trail following behaviour.

The species specificity of trail tracking behaviour

Townsend (1974b) found that *Biomphalaria glabrata* would not follow trails laid by *Lymnaea stagnalis* and suggested that trail following might be triggered by a pheromone. However, of the nine species tested in the present study, trails laid by two planorbids, *B. pfeifferi* and *Planorbella (Seminolina) duryi*, induced marked tracking behaviour, while trails laid by another three species, two planorbids (*B. tenagophila* and *Planorbis planorbis*) and a physid (*Physella acuta*), produced weaker, though still statistically significant, effects. It appears, then, that whatever the necessary quality is, it is not restricted to mucus produced by a single species, or even a single snail family. In addition, it is clear that mucus trail tracking is not an all-or-nothing phenomenon. The tendency for *B. glabrata* to follow mucus trails laid by other species is a graded quantity, as is, presumably, the stimulus that triggers this form of behaviour. In this context, it is interesting to note that the species *Physella acuta* will follow trails laid by conspecifics (Wells & Buckley, 1972), and that both *B. pfeifferi* and *B. tenagophila* will follow their own trails, as well as those of *Planorbella (S.) duryi* (Tait & Bousfield, unpubl. observ.). In contrast, following of conspecific trails is a very rare occurrence in all the lymnaeids tested in these experiments (Towner-Jones, unpubl. observ.). It may be, then, that a common factor is involved in triggering trail following for all species which demonstrate this type of response.

The effects of diet on trail tracking

It has been postulated that the nature of the snails' diet might affect the quality of the mucus trail they produce and, consequently, their attractiveness to tracker snails. Some circumstantial support for this hypothesis is provided by the observations that the mucus of the pulmonate snails *Lymnaea truncatula* (Wilson, R.A., 1968) and *Helix aspersa* (Campion, 1961) contain metabolites characteristic of plant material. In the case of some insects, there is evidence that sex pheromones are closely related to compounds found in the diet, and it has been suggested that dietary differences between populations could result in reproductive isolation and subspeciation (Hendry, 1976). However, the present results do not support the above hypothesis, as no differences could be detected in the extent to which lettuce-fed *Biomphalaria glabrata* follow trails deposited by snails fed on lettuce, *Rorippa* and *Apium*. Townsend (1974b) also found that lettuce-fed *B. glabrata* will follow trails deposited by cellulose-fed snails, despite the fact that the cellulose diet is deficient in a large number of nutrients present in lettuce (Stanislawski & Becker, 1979). It can be concluded, therefore, with Townsend (1974b) that, if there is a chemical factor involved in trail following by *B. glabrata*, its nature does not appear to be influenced by diet.

A brief period of anoxia produced the most highly 'active' trails observed during the course of these experiments. This effect of anoxia on mucus trail tracking was not specific to *Biomphalaria glabrata*, for it also was observed, albeit at a smaller magnitude, for *Lymnaea stagnalis* marker snails treated in a similar manner (Tables 2ii, 3).

Taken together, the results of the experiments discussed so far suggest that the feature of mucus which triggers tracking is of quite general distribution throughout basommatophoran molluscs and that it can be affected by quite modest periods of isolation from food or by anoxia.

Mechanisms underlying the waning period

If trail following is triggered by the presence of low molecular weight metabolites present in the mucus matrix, then it follows that the gradual diffusion of this component could account for the waning period. The experimental evidence at first sight suggests that this is not the case.

The results of the experiments performed on Tygan mesh suggest that either the active factor does not diffuse or, alternatively, that it does not reach sufficiently high a concentration over the 5-10 min interval allowed for re-establishment of chemical gradients to stimulate following.

Bossert & Wilson (1963) have produced a theoretical analysis of pheromone concentrations and their spatial and temporal distributions in a variety of situations. In particular, their formulae developed to describe the behaviour of a substance released continuously in a wind can be adapted to provide insight into the distribution of a diffusing chemical about a perfectly straight mucus trail laid on a flat plane. Under these circumstances:

$$U(r,t) = \frac{Q}{2\pi DX} \cdot \exp(-ur^2/4DX) \qquad (1)$$

where **t** is the age of the mucus a distance x behind a snail moving with uniform velocity **u** along the x-axis of a rectangular coordinate system ($u/x = 1/t$). $r(r^2 = x^2 + y^2)$ is the distance from the mucus at which the concentration U(r,t) of chemical is to be calculated. **D** is the diffusion constant of the chemical and **Q** is the number of molecules of stimulant originally present in unit length of trail. Bossert and Wilson found it convenient to consider the spatial and temporal behaviour of the 'active space', which was defined as the surface within which U(r,t) was greater than **K**, the behavioural threshold concentration for trail following.

The behaviour of diffusing mollecules in water is far different from that of the same substance in air (Wilson, E.O., 1970). The diffusion constants of most water-soluble substances are of the order of 10^{-5} (amino acids and similar sized molecules) to 10^{-7} (proteins), while in air volatile substances have diffusion constants ranging from 10^{-1} to 10^{-2} cm^2/sec (Wilson, E.O., 1970; Lehninger, 1977). Consequently, the characteristic spatial and temporal dimensions of diffusion in water are considerably different from those measured in air. From equation 1, it is a simple matter to calculate the maximum length of the active space, X_{max}, together with its maximum height above the substrate, R_{max}. Thus:

$$X_{max} = Q/2K\pi D \qquad (2)$$

$$R_{max} = \sqrt{\frac{2Q}{eK\pi u}} \qquad (3)$$

where **e** is the base of the natural logarithm. Taking $D = 10^{-5}\,cm^2/sec$, $u = 5cm/min$, and $T_{max} = 20$ min, we calculate that $X_{max}(= u.T_{max}) = 100$ cm and, therefore, by elimination of the quantity of Q/K in equation 3, that R_{max} is of the order of 2.10^{-2} cm. This is the maximum value which can be obtained using the range of diffusion constants given above. This distance is of the same order of magnitude as the thickness of the mesh used to cover the trails. Thus, even in the absence of the physical disruption caused by mesh placement, it would be unlikely for the active space to extend further than this. To a first approximation, therefore, the active space extends no further than the surface of the mucus itself, so that its presence only may be sensed when the tracker snail is in physical contact with it. This observation may partially explain the negative findings of the second series of experiments investigation the role played by diffusion in limiting trail life.

Fick's law states that, in an isotropic medium, the rate of diffusion of a solute across a boundary is proportional to the concentration gradient across it (Lehninger, 1977). A flow

of water over the surface of the trail would, by removing diffused substances from the water-mucus interface, therefore increase this rate of loss and, consequently, if diffusion were the rate-limiting factor, reduce the waning time. This was found not to be the case.

It was assumed above that the medium in which diffusion was occurring was isotropic. That is to say, the physical properties of the medium were the same on both sides of the boundary being considered. This is unlikely to be the case for a mucus-water interface. In a mucus gel where most of the solvent is inter-molecular, the diffusion of even small molecules may be reduced (Clamp et al., 1978) and the numerous 'binding sites' on the glycoprotein molecules themselves may impede further the movement of a solute, particularly if this molecule possesses highly polar or non-polar regions (Clamp et al., 1978). The diffusion constant within the mucus, therefore, would be much less than that in water alone, and under these circumstances loss of the substance would be determined largely by the properties of the mucus itself, and would be relatively unaffected by external factors such as currents (Cardarelli, 1977).

It is possible that the gradual loss of activity be attributable to changes in the physical properties of the mucus, as the relatively weak forces which give rise to the three dimensional structure of mucus may be disturbed quite easily (Clamp et al., 1978). It is known, for example, that some purified vertebrate glycoproteins aggregate spontaneously, while others apparently gradually 'disentangle' themselves (Sadé et al., 1975; Creeth et al., 1977). Also, addition of certain inorganic ions, especially divalents, can have large effects on the physical properties of mucus, and the evidence suggests that calcium can bind to snail glycoproteins (Ogston, 1976) and influence viscosity (Gray, 1926). Since the viscous, elastic and thixotropic properties of mucus play a crucial part in dictating the speed and efficiency of ciliary locomotion (Blake & Sleigh, 1974; Sleigh, 1974; Clamp et al., 1978; Creeth, 1978), any changes that might occur should be apparent by comparison of tracker snail speeds of movement. Since significant differences in velocity were not found for snails tracking 3 and 15 min old trails, it may be assumed that these changes, if they occur, do not directly give rise to the waning effect (see Table 6). A similar conclusion follows from the comparison of overlap lengths and tracking speeds obtained in the deprivation and anoxia experiments (see Table 2iii).

Finally, it is interesting to note that technological advances in the use of solid, elastomeric matrices capable of releasing water-soluble compounds into an aquatic environment at controlled rates and for long periods of time have led to renewed interest in the chemical control of intermediate hosts of human schistosomiasis, such as *Biomphalaria glabrata* (Cardarelli, 1977; Uhazy et al., 1978). If the explanations concerning the physical and chemical basis of mucus trail tracking behaviour offered above are correct, then it would appear that snail mucus is itself a 'slow release matrix'.

Possible metabolites underlying mucus trail tracking behaviour

Aquatic snails release a wide range of substances into the surrounding water, and many of these metabolites may be present in the mucus at quite high concentrations. The mucus of *Lymnaea truncatula*, for example, contains a large number of free amino acids (overall concentration, 7mM; concentration of the most abundant amino acid, arginine, 1.88mM), together with a number of free fatty acids (overall concentration, 5mM) (Wilson, R.A., 1968). Formic, acetic, propionic and butyric acids have been identified in mucus collected from *Biomphalaria glabrata* (Simpson & Chamberlain, pers. comm.). The free amino acid content of this mucus has not been assayed, but it is known that *B. glabrata* releases amino acids from its body under normal circumstances (MacInnis et al., 1974).

For many invertebrates, the products of aerobic and anaerobic metabolism include a variety of organic acids, some of which subsequently may be expelled from the organism (Simpson & Awapara, 1966; Hochachka & Mustafa, 1972; Zwaan & Wijsman, 1976). Thus, in

addition to lactate (Selkurt, 1966; Schmidt-Nielsen, 1975), considerable quantities of succinate, acetate and propionate, plus the amino acid alanine, may accumulate in the body during periods of hypoxia and result in an increase in the rate of excretion of short chain fatty acids, such as propionate or acetate (Zwaan & Wijsman, 1976; Surholt, 1977; Gruner & Zebe, 1978). Von Brand et al. (1950) have suggested that fermentation of carbohydrate forms an essential component of *Biomphalaria glabrata*'s respiratory metabolism under both aerobic and anaerobic conditions. In addition, they have shown that the tissue concentration of end products of carbohydrates falls during starvation (von Brand et al., 1946) and rises during periods of anoxia (von Brand et al., 1950). Von Brand and colleagues (von Brand et al., 1946; von Brand et al., 1950; von Brand & Mehlman, 1953) also have demonstrated that different families of snail produce differing quantities of lactic acid during anaerobiosis. Lymnaeids and physids, for example, showed a marked accumulation of this substance in their tissues, whereas planorbids produced mainly other, unidentified products.

As a result of screening a wide range of amino, fatty and other organic acids, Thomas and colleagues (Thomas & Assefa, 1979; Thomas et al., 1980; Thomas et al., 1981) have found that adult *Biomphalaria glabrata* are principally attracted by propionate and butyrate, whereas lactate is comparatively ineffective. Substances such as these therefore could be important stimuli triggering mucus trail tracking.

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A SECOND FINDING OF *BULINUS TRUNCATUS* IN JORDAN. – The threat of schistosomiasis to Jordan was thought to be minimal prior to 1975. This was based mainly on (1) the fact that the patients diagnosed in Jordan had encountered the disease in neighbouring countries, and (2) the absence of the snail intermediate hosts as determined by the limited surveys of Abdel Azim & Gismann (1956) and Chu (1969). The report by Saliba et al. (1976) on the presence of *Bulinus truncatus* (Audouin) in a limited area in the Jordan Valley, after diagnosis of an allegedly autochothonus case of urinary schistosomiasis, showed that transmission of the disease is possible and probable.

This communication reports on the occurrence of *Bulinus truncatus*, an intermediate host of *Schistosoma haematobium* (Bilharz), in another site in Jordan. Initially, the site was investigated by Bandel and Salameh (Department of Geology and Mineralogy, University of Jordan, Amman, Jordan) during a hydrochemical study of the catchment area of the Zarqa River. Their recovery of dead shells of snails of suspected medical importance prompted this investigation during late 1978 and early 1979, which led to the recovery of living *B. truncatus* snails from a site near the town of Jarash.

Description of the site. The site where the snails were found is a spring and its drainage canals about 2 km to the north of Jarash, a town famous for its Roman ruins (Fig. 1). The spring has been in existence for a long period of time since a Roman pool was built there (Fig. 2). The pool is 100 m in length, 40 m in width and 3.5 m in depth and is divided into two parts by a stone wall. Water emerges from several points along the northern end of the pool. Due to the unevenness of its muddy bottom and the continuous overflow of water from the pool into its drainage canals, the water depth varies from 0.5 to 1.0 m.

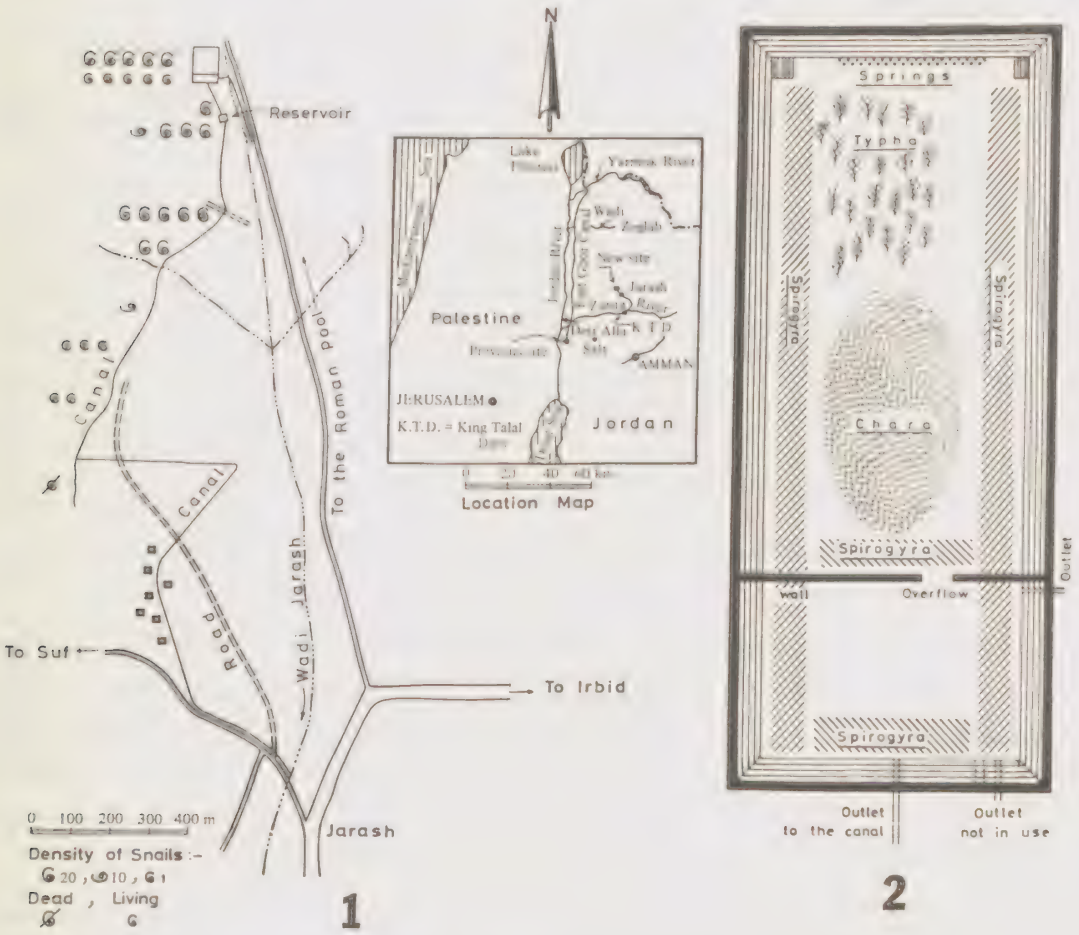

FIG. 1. The canal from the Roman pool to its discharge in Wadi Jarash. FIG. 2. The Roman pool.

The water is utilized mainly for irrigation. A main cement canal (50 cm in depth and 30 cm in width) that runs almost 2.5 km carries the water from the pool to different plots of irrigated land. However, excess water, especially in winter, reaches the Wadi of Jarash through this canal, as well as through a second water outlet at the eastern side of the pool. Wadi Jarash, in turn, discharges into the Zarqa River, which runs into the recently built King Talal Dam. Water in the dam flows westward and reaches the River Jordan, occasionally overflowing into the East Ghor Canal, which brings water from the Yarmouk River at the northern borders of Jordan.

Findings. In addition to the presence of *Bulinus truncatus* snails, which will be discussed later in detail, thousands of *Melanopsis* and a few *Valvata* and *Hydrobia* snails were also encountered in the pool. Furthermore, annelids, crustaceans, aquatic insects, frog tadpoles and fishes lived in the pool. As seen from Fig. 2, two types of algae, *Spirogyra* and *Chara*, as well as *Typha* grass, were present also.

Few living *Bulinus truncatus* snails were collected from the pool, mainly attached to *Chara*. However, large numbers of shells were obtained from the muddy bottom of the pool when investigated by dipping. An average number of 1.4 shells per dip was obtained. The shells were of different sizes and ranged from 5-11 mm in length, with an average length of 6.8 mm. The shell color varied from dark green to white as a result of various degrees of bleaching.

A thorough survey of the cemented drainage canal revealed that *Bulinus truncatus* snails existed in a cement reservoir adjacent to a pump house about 100 m east of the pool, as well as in the drainage canal some 450 m from the pool (Fig. 1). The snails were seen attached to small stones and to *Cladophora* algae present in the canal. Few snails were seen at points up to 1.5 km from the pool. Shells, however, were collected at further distances. *Melanopsis* snails were found only in the first 300 m of the canal. None of the *B. truncatus* collected were infected with larval stages of trematodes.

The following ions with their respective concentrations were obtained when a sample of the pool water was chemically analyzed, either spectrophotometrically or by titration (in ppm): Ca, 72; Mg, 39; Na, 38; K, 2; Cl, 146; SO_4, 53; NO_3, 24; HCO_3, 171; total dissolved ions, 545; (in ppb): Fe, 8; Mn, 0.2; Cu, 6; and Cd, 0.6.

Discussion. The finding of *Bulinus truncatus* in this site, in addition to its earlier recording by Saliba et al. (1976) near Deir Alla village, clearly shows that this snail may become established in Jordan. This poses the threat that urinary schistosomiasis also might become endemic, since thousands of infected foreign laborers are present in the country (Saliba et al., 1980).

The origin of the snails is not yet known, and their introduction into this site most probably is not very recent. The presence of large numbers of shells of different sizes and the weathering of those shells support this notion. A few months before this investigation began, fishes were brought from Azraq oasis in the Jordanian desert to the pools. No *Bulinus*, however, were found in the area from which the fishes were brought. Furthermore, the staff of the Malaria Control Division have been adding the insecticide Abate to the pool to control mosquito breeding (Mohammad Reda Tawfiq, pers. comm.). This might have unfavorably affected the snail population in this site and contributed to the large number of shells observed.

The chemical characteristics of the pool water are within the limits tolerated by the snail and other aquatic forms (fishes, frogs, plants, etc.). The water is considered by the villagers living close-by as acceptable, to the extent that children swam there and women used it for various domestic purposes except drinking and cooking.

The possibility that water from the pool as well as its drainage canal could reach Wadi Jarash and thus the Zarqa River poses the threat that snails could be dispersed from this site to other water bodies in the country.

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ANNUAL REPORTS AND BULLETINS OF THE AMERICAN MALACOLOGICAL UNION

Since 1968, the contents of the *Annual Reports* or *Bulletins* of The American Malacological Union have been published regularly in the "*Contents* of current malacological periodicals" section of *Malacological Review*. This coverage began with *The American Malacological Union, Inc., Annual Reports for 1967*, Bulletin No. 34.

The contents of the *Annual Reports* for the years 1931-1966 are given below, i.e., the contents of those reports from the initiation of The American Malacological Union to the year that *Malacological Review* began covering the contents of the society's publications. Preceding these contents of the early annual reports is a complete list of the reports.

Year	Annual meeting	Report or Bulletin cover title	Bulletin No.	Publication date
1931	1st	Members of the American Malacological Union	[1]*	April 1, 1932
1932	2nd	Mrs. Imogene C. Robertson's rambling notes on the Second Annual Meeting of the American Malacological Union in Washington, D.C., May 26-28, 1932	[2]	
1933	3rd	[Apparently no report was published for the Third Annual Meeting]	–	
1934	4th	Report - Fourth Annual Meeting and membership, the American Malacological Union	[3]	August 1, 1934
1935	5th	Report - Fifth Annual Meeting and membership, the American Malacological Union, June 27-29, 1935	[4]	
1936	6th	The American Malacological Union, Sixth Annual Meeting, Saint Petersburg, Florida, April 21-24, 1936. Membership list, revised September 1, 1936	[5]	
1937	7th	The American Malacological Union, Seventh Annual Meeting, University of Michigan Museum, Ann Arbor, Michigan, August 3-5, 1937. Membership list, revised, January 1, 1938	[6]	1938
1938	8th	The American Malacological Union, Eighth Annual Meeting, University of Havana, Havana, Cuba, August 1-6, 1938. Membership list, revised, January 1, 1939	[7]	1939
1939	9th	The American Malacological Union, Ninth Annual Meeting, Royal Ontario Museum of Zoology, Toronto, Ontario, June 20-23, 1939. Membership list, revised, December, 1940	[8]	
1940	10th	The American Malacological Union, Tenth Annual Meeting, Academy of Natural Sciences, Philadelphia, Pennsylvania, June 17-21, 1940. Membership list revised, December, 1940	[9]	

*Bulletin numbers in brackets are the numbers assigned retroactively from Bulletin 22, 1955, the first Report to receive a "bulletin number".

1941	11th	The American Malacological Union, The Eleventh Annual Meeting, Rockland and Thomaston, Maine, August 26-29, 1941. Papers presented at the Symposium on Methods of Collecting and Preserving Mollusks, Wednesday, August 27, 1941. Membership list revised January, 1941	[10]	
1942	–	[No meeting or publication]		
1943	–	The American Malacological Union, News bulletin and annual report, 1943. Membership list revised, January, 1944	[11]	1944
1944 1945		The American Malacological Union, News bulletin and annual report, 1944-45. Membership list revised, October, 1945	[12]	
1946	12th	News bulletin and annual report, 1946, the American Malacological Union. Membership list revised, April 1947	[13]	1947
1947	13th	The American Malacological Union, News bulletin and annual report, 1947. Membership list revised, December, 1947	[14]	
1948	14th	The American Malacological Union, News bulletin and annual report, 1948. Membership list revised, March, 1949	[15]	1949
1949	15th	The American Malacological Union, News bulletin and annual report, 1949. Membership list revised, November, 1949	[16]	
1950	16th	The American Malacological Union, News bulletin and annual report, 1950. Membership list revised, December, 1950	[17]	
1951	17th	The American Malacological Union, News bulletin and annual report, nineteen hundred and fifty one. Membership list revised, December, 1951	[18]	
1952	18th	The American Malacological Union, annual report 1952, eighteenth annual meeting. Pacific Division (A.M.U.P.), fifth annual meeting. Membership list revised, December, 1952	[19]	
1953	19th	American Malacological Union and American Malacological Union, Pacific, Division, Annual Report	[20]	December 31, 1953
1954	20th	The American Malacological Union, Annual Report 1954, Twentieth Annual Meeting. American Malacological Union - Pacific Division, Seventh Annual Meeting. Membership list revised December, 1954	[21]	
1955	21st	The American Malacological Union, founded 1931, The American Malacological Union Pacific Division, founded 1948, Annual reports for 1955. A.M.U. Twenty-first Annual Meeting, A.M.U., P.D. Eight Annual Meeting. Membership list revised, December 31, 1955	22	December 31, 1955
1956	22nd	25th anniversary issue, the American Malacological Union, founded 1931, the American Malacological Union, Pacific Div., annual reports 1956, 22nd meeting, A.M.U., 9th meeting, A.M.U., P.D. (combined meeting). Membership list revised. December 31, 1956	23	December 31, 1956

1957	23rd	The American Malacological Union, founded 1931, the American Malacological Union, Pacific Division, founded 1948, Annual reports for 1957, A.M.U., twenty-third annual meeting, A.M.U., P.D., tenth annual meeting	24	January 1, 1958
1958	24th	The American Malacological Union, founded 1931, The American Malacological Union, Pacific Division, founded 1948, Annual reports for 1958, A.M.U., twenty-fourth annual meeting, A.M.U., P.D., eleventh annual meeting. Membership list revised December 31, 1958	25	January 1, 1959
1959	25th	The American Malacological Union, founded 1931, the American Malacological Union, Pacific Division, founded 1948, Annual reports for 1959, A.M.U., twenty-sixth annual meeting, A.M.U., P.D., Twelfth Annual Meeting. Membership list revised November 15, 1959. [Actually A.M.U. 25th meeting]	26	January 1, 1960
1960	26th	The American Malacological Union, The American Malacological Union, Pacific Division, Annual reports for 1960, A.M.U., Twenty-seventh Annual Meeting, A.M.U., P.D., Thirteenth Annual Meeting. [A.M.U. 26th meeting]	27	January 1, 1961
1961	27th	The American Malacological Union, The American Malacological Union, Pacific Division, Annual reports for 1961, A.M.U., Twenty-eighth Annual Meeting, A.M.U., P.D., Fourteenth Annual Meeting. [A.M.U. 27th meeting]	28	December 1, 1961
1962	28th	The American Malacological Union, The American Malacological Union, Pacific Division, Annual reports for 1962, A.M.U., Twenty-ninth Annual Meeting, A.M.U., P.D., Fifteenth Annual Meeting. [A.M.U. 28th meeting]	29	December 1, 1962
1963	29th	The American Malacological Union, The American Malacological Union, Pacific Division, Annual reports for 1963, A.M.U., Twenty-ninth Annual Meeting, A.M.U., P.D., Sixteenth Annual Meeting	30	December 1, 1963
1964	30th	The American Malacological Union, Inc., The American Malacological Union, Pacific Division, Annual reports for 1964, AMU, Thirtieth Annual Meeting, AMU, PD, Seventeenth Annual Meeting	31	December 1, 1964
1965	31st	The American Malacological Union, Inc., The American Malacological Union, Pacific Division, Annual reports for 1965, AMU, Thirty-first Annual Meeting, AMU, PD, Eighteenth Annual Meeting	32	December 1, 1965
1966	32nd	The American Malacological Union, Inc., The American Malacological Union, Inc., Pacific Division, Annual reports for 1966, AMU, Thirty-second Annual Meeting, AMU, PD, Nineteenth Annual Meeting	33	December 1, 1966
1967	33rd	The American Malacological Union, Inc., The American Malacological Union, Inc., Pacific Division, Annual reports for 1967, AMU, Thirty-third Annual Meeting, AMU, PD, Twentieth Annual Meeting	34	March 20, 1968

1968	34th	The American Malacological Union, Inc., The American Malacological Union, Inc., Pacific Division, Annual reports for 1968, AMU, Thirty-fourth Annual Meeting, AMU, PD, Twenty-first Annual Meeting	35	December 28, 1968
1969	35th	The American Malacological Union, Inc., The American Malacological Union, Inc., Pacific Division, Annual reports for 1969, AMU, Thirty-fifth Annual Meeting	36	December 19, 1969
1970	36th	The American Malacological Union, Inc., The American Malacological Union, Inc., Pacific Division, Annual reports for 1970, AMU, Thirty-sixth Annual Meeting	37	February 18, 1971
1971	37th	The American Malacological Union, Inc., Bulletin for 1971, AMU, Thirty-seventh Annual Meeting	[38]*	February, 1972
1972	38th	The American Malacological Union, Inc., Bulletin for 1972, AMU, Thirty-eighth Annual Meeting	[39]	March 23, 1973
1973	39th	The American Malacological Union, Inc., Bulletin for 1973, AMU Thirty-ninth Annual Meeting	[40]	May, 1974
1974	40th	The American Malacological Union, Inc., Bulletin, 1974, Fortieth Annual Meeting	[41]	May, 1975
1975	41st	Bulletin of The American Malacological Union, Inc., for 1975. Joint Meeting of The Western Society of Malacologists, Eighth Annual Meeting, The American Malacological Union, Forty First Annual Meeting, San Diego, California, 22-26 June 1975	[42]	January 30, 1976
1976	42nd	Bulletin of The American Malacological Union, Inc., for 1976. Forty Second Annual Meeting, Columbus, Ohio, 2-6 of August 1976. The American Malacological Union	[43]	December 30, 1976
1977	43rd	Bulletin of The American Malacological Union, Inc., for 1977. Forty Third Annual Meeting, Naples, Florida, July 10-15, 1977. The American Malacological Union	[44]	
1978	44th	Bulletin of The American Malacological Union for 1978. Covering the Forty Fourth Annual Meeting, Wilmington, North Carolina, July 16-21, 1978	[45]	
1979	45th	Bulletin of The American Malacological Union for 1979. Covering the Forty Fifth Annual Meeting, Corpus Christi, Texas, August 5-11, 1979. Joint meeting with Western Society of Malacologists	[46]	
1980	46th	Bulletin of The American Malacological Union for 1980. Covering the Forty Sixth Annual Meeting, July 19-25, 1980, Louisville, Kentucky	[47]	

*After Bulletin 37, the annual issues of the Bulletin have not been officially assigned "bulletin numbers"; and, after the year 1976, a publication date has not been given.

MEMBERS

OF THE

AMERICAN

MALACOLOGICAL UNION

APRIL 1, 1932

CONSTITUTION OF THE AMERICAN MALACOLOGICAL UNION

Adopted April 30, 1931

1. This Society shall be called "The American Malacological Union.

2. Its object shall be the promotion of the science of malacology by holding meetings for reading and discussion of papers, and for furthering the interests of students and collectors of shells by facilitating acquaintance and co-operation among the members.

3. Membership shall be limited to persons resident in the Americas and Hawaii. New members may be proposed by two members and balloted for by the Council. They shall pay an annual subscription of $1.00. They will receive without other charge all notices, programs, lists of members, etc., issued by the Union.

4. The following officers shall be elected annually by ballot: President, Vice-President, two Secretaries, Treasurer.

5. The Union will be governed by a council consisting of the officers and four other members to be elected annually by ballot.

6. The annual meeting shall be held at such time and place as may be fixed by the preceding annual meeting. Other meetings may be called by the Council. Meetings of local branches may be held as such branches may determine.

7. Proposals for the alteration of this constitution when signed by five members and passed by the Council shall be acted upon at the next annual meeting. Concurrence of three-fourths of the ballots cast are necessary for any alteration.

8. THE NAUTILUS is hereby designated as the official organ of the Union.

Mrs. Imogene C. Robertson's
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American Malacological Union in Washington, D. C.
May 26-28, 1932

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THE AMERICAN MALACOLOGICAL UNION

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AUGUST 1, 1934

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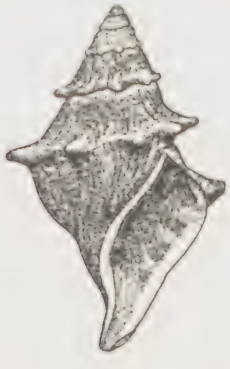

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-and-

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THE AMERICAN MALACOLOGICAL UNION

THE ELEVENTH ANNUAL MEETING

ROCKLAND AND THOMASTON, MAINE

AUGUST 26 --- 29, 1941

Papers Presented at the Symposium on

METHODS of COLLECTING and PRESERVING MOLLUSKS

Wednesday, August 27, 1941

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It is with regret that we are obliged to announce that there will be no annual meeting this year.

An invitation to Washington was accepted but it soon became apparent that a meeting in that city could not be successfully arranged due to war conditions. Sanibel was next in order, and plans were begun to hold the meeting there in April. However, with war conditions extended to the entire country and transportation problems daily becoming more acute, it has been thought best, after much consultation among the members of the Council, to suspend meetings for the duration of the war.

THE AMERICAN MALACOLOGICAL UNION

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AND

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The American Malacological Union, Pacific Div.
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25th ANNIVERSARY ISSUE

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FOUNDED 1931

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FOUNDED 1948

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THE AMERICAN MALACOLOGICAL UNION,

PACIFIC DIVISION FOUNDED 1948

A. M. U., Twenty-fourth Annual Meeting
A. M. U., P. D., Eleventh Annual Meeting

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A.M.U., Twenty-eighth Annual Meeting
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THE AMERICAN MALACOLOGICAL UNION

ANNUAL REPORTS for 1963

The American Malacological Union
Pacific Division

A.M.U., Twenty-ninth Annual Meeting
A.M.U., P.D., Sixteenth Annual Meeting

And to forestall mass protest that the twenty-ninth annual meeting was held in 1962, hence that of 1963 was the thirtieth, the editorial staff confesses that an error was made in 1959 when the cover caption of Annual Report Bulletin Number 26 listed the twenty-sixth annual meeting rather than (properly) the twenty-fifth. The error was perpetuated without detection until the current year at which time several alert subscribers noticed and reported it. Historians please note: the 1964 annual meeting of the American Malacological Union will be the thirtieth!

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ANNUAL REPORTS for 1965

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Pacific Division

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NEWS AND ANNOUNCEMENTS

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THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND. – The program for the Society for the 2nd half of the year 1981 is as follows: *Exhibitions* - Tropical freshwater bivalves (Oct. 17); Tropical marine bivalves (Nov. 14); Shell artifacts (Dec. 12). *Discussions* - A.J. Brook, 'Algae and freshwater Mollusca' (Oct. 17); John Llewellyn Jones, 'Cockles and mussels alive, alive O!' (Nov. 14); Eleanor Fogan, 'Architectural molluscs' (Dec. 12). *Field meetings* - West Runton, Norfolk (July 11); Joint meeting with the Northampton Natural History Society (July 26); Pashford Pens Fen, Barton Mills, Suffolk (Sept. 12); Rhossili, Gower (Sept. 19); Autumn slug foray, Midhurst district of the Weald (Oct. 18). Regular meetings of the Society are held in The British Museum (Natural History), Cromwell Road, South Kensington, London, SW7, at 2:30 p.m. in the Demonstration Room.

MEETING OF THE INSTITUTE OF MALACOLOGY. – The annual meeting of the Institute of Malacology was held in the Museum of Zoology, The University of Michigan, Ann Arbor, U.S.A., on April 24, 1981. The meeting was presided over by the President, Clyde F. E. Roper. Others attending were Christopher J. Bayne, J.B. Burch, Melbourne R. Carriker, George M. Davis, Robert Robertson, W.D. Russell-Hunter and S.K. Wu. The main business discussed was the affairs of *Malacologia*, which is published by the Institute of Malacology. The following are the new officers of the Institute: President, Christopher J. Bayne; President-Elect, S.K. Wu; Vice President, W.D. Russell-Hunter. George M. Davis continues as Secretary-Treasurer.

MEETINGS OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1980 annual business meeting of the Society for Experimental and Descriptive Malacology was held in February, 1980, in Ann Arbor, Michigan, U.S.A. An interim business meeting of the Society was held on 25 August 1980 in Ann Arbor. The 1981 annual business meeting was held in Ann Arbor on April 29, 1981. The time and place of the 1982 annual business meeting will be announced in early 1982.

MALACOLOGY COURSE IN THE PHILIPPINES, 1980, 1981. – On 5-28 May 1980, a National Training Course on Medical Malacology was given in the Philippines (Manila and Sorsogon) by Dr. J.B. Burch, The University of Michigan, Ann Arbor, Michigan, U.S.A., Dr. B.C. Dazo, World Health Organization, Western Pacific Region, Dr. Edito G. Garcia and Prof. Nonette C. Jueco, Institute of Public Health, University of the Philippines, Dr. Ruben Umaly, Department of Zoology, University of the Philippines, and Dr. Roger Abear, Dr. Julian Noseñas and Mr. Manuel Santos, Schistosomiasis Control and Research Service, Ministry of Health, Manila. The course was sponsored by the Schistosomiasis Research and Control Service, Ministry of Health, Manila, and supported by the World Health Organization, Regional Office for the Western Pacific, Manila, Philippines. The course comprised lectures, laboratory practical exercises and field trips, and covered various aspects of molluscan biology, including classification, geological history, zoogeography, evolution, anatomy, physiology (respiration, feeding and digestion, excretion and endocrinology), reproduction, genetics, cytogenetics and cytotaxonomy, medical malacology (snails and trematodes of medical importance, epidemiology of snail-mediated diseases, chemotherapy, and snail surveillance and control), laboratory and field methods, and research methodology. In July 1981, a second National Training Course on Medical Malacology will be given in the Philippines by the same lecturers.

SUMMER 1982 MALACOLOGY COURSE AT THE UNIVERSITY OF MICHIGAN. – The Division of Biological Sciences of The University of Michigan will offer a course in "Biology of Mollusks" (Zoology 438) during the 1982 summer half-term (July to mid-August). This course will be open to both undergraduate and graduate students. For information regarding registration, write to Admissions Office, 1220 Student Activities Building, The University of Michigan, Ann Arbor, Michigan 48109. For information on course content, write to Dr. J.B. Burch, Department of Ecology and Evolutionary Biology, Division of Biological Sciences, The University of Michigan, P.O. Box 2749, Ann Arbor, Michigan 48106, U.S.A.

MALACOLOGICAL REVIEW, SUPPLEMENTS 1 AND 2. – Supplements 1 and 2 are available from *Malacological Review* at the prices given below. They can be ordered from *Malacological Review*, P.O. Box 2750, Ann Arbor, Michigan 48106, U.S.A.

Supplement 1. *Freshwater snails of Taiwan (Formosa)*, by Gary L. Pace. This illustrated monographic study deals with the identification, classification, distribution, zoogeographic affinities and parasitological importance of thirty-nine species of Formosan freshwater gastropod mollusks. US$15.00, postpaid.

Supplement 2. *The Mekong Schistosome*, J.I. Bruce, S. Sornmani, H.L. Asch & K.A. Crawford, Editors. This publication is a monograph on the newly discovered human blood fluke, *Schistosoma mekongi*, and its unusual molluscan host, *Tricula aperta*. In addition to details on the parasite, this book presents various studies on the snail intermediate host, including its anatomy, systematic and zoogeographic relationships, evolution, habitats and bionomics, laboratory maintenance and culture, susceptibility to the parasite, effect of the parasite on the snail, the snails' role in disease transmission, and sensitivity of the snails to molluscicides. US$26.00, postpaid.

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(già *Conchiglie*)

PUBBLICAZIONE MENSILE EDITA DALLA
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COVERING THE FORTY SIXTH ANNUAL MEETING

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(Gastropoda)

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Leipzig

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Wien

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ALEXANDRU V. GROSSU
Bukarest

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A MAGYARORSZÁGI RECENS PUHATESTŰEK ELTERJEDÉSE

S O O S I A N A
/SUPPL. I./

1979

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Distribution des mollusques actuels de la Hongrie

Die Verbreitung der rezenten Mollusken Ungarns

Распространение современных моллюсков Венгрии

László P i n t é r
Andor R i c h n o v s z k y
Anna S. S z i g e t h y

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clarissimi doctoris
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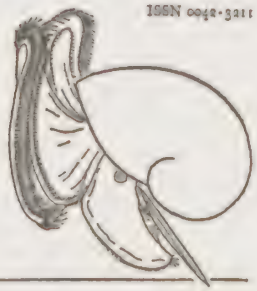

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